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Editor: JOHN M. COULTER

March 1913

Inheritance of Flower Size in Crosses between Species of Nicotiana — E. M. East

The Climax Forest of Isle Royale, Lake Superior, and Its Development. III — William S. Cooper

Studies on the Phloem of the Dicotyledons — Ansel F. Hemenway

Paraffin Blocks for Growing Seedlings in Liquid Culture Solutions — Conrad Hoffmann

Briefer Articles

A Simple Revolving Table for Standardizing Porous Cup Atmometers — G. E. Nichols

Poisoning by Ginkgo — Anna M. Starr

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Vol. LV — CONTENTS FOR MARCH 1913 — No. 3

INHERITANCE OF FLOWER SIZE IN CROSSES BETWEEN SPECIES OF NICOTIANA (WITH PLATES VI–X). *E. M. East* - - - - - - - - - - - - - - - - 177

THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. I. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 165 (WITH TWENTY-FIVE FIGURES). *William S. Cooper* - - - - - - - - - - - - - - - 189

STUDIES ON THE PHLOEM OF THE DICOTYLEDONS. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 169 (WITH PLATE XI AND THREE FIGURES). *Ansel F. Hemenway* 236

PARAFFIN BLOCKS FOR GROWING SEEDLINGS IN LIQUID CULTURE SOLUTIONS (WITH THREE FIGURES). *Conrad Hoffmann* - - - - - - - - - - - - - - 244

BRIEFER ARTICLES

A SIMPLE REVOLVING TABLE FOR STANDARDIZING POROUS CUP ATMOMETERS (WITH ONE FIGURE). *G. E. Nichols* - - - - - - - - - - - - - - - - - - 249

POISONING BY GINKGO. *Anna M. Starr* - - - - - - - - - - - - - - - - - 251

CURRENT LITERATURE

BOOK REVIEWS - 252

PARASITIC SEED PLANTS. PHOSPHORESCENCE IN PLANTS

MINOR NOTICES - 254

NOTES FOR STUDENTS - 254

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VOLUME LV NUMBER 3

THE

BOTANICAL GAZETTE

MARCH 1913

INHERITANCE OF FLOWER SIZE IN CROSSES BETWEEN SPECIES OF NICOTIANA[1]

E. M. EAST

(WITH PLATES VI–X)

Since the independent investigations of NILSSON-EHLE and of the writer demonstrated the feasibility of using the Mendelian notation to describe the inheritance of size characters that blend in the first hybrid generation, a number of botanical papers have appeared that supported this interpretation. These papers have considered the behavior in crosses of such characters as height of plant, size of leaf, number of leaves, time of flowering, and size of fruit. If the number of leaves in certain plants is excluded, this type of character is one particularly affected during development by external conditions. Since fluctuations produced in this manner are not transmitted, if the conclusions drawn from the sum total of our limited experimental cultures are to be given weight, the validity of the evidence in these investigations is not disturbed. At the same time, one must admit that these fluctuations obscure an analysis of the crude data. For example, plant *B* may be six inches higher than plant *A* when both are grown in the same environment, owing to a different heritage, but plant *A* may grow considerably higher than plant *B* if the environment of *A* is the best possible for maximum growth and the environment of *B* is poor.

In this paper, therefore, I propose to consider the inheritance of

[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

a character-complex which I believe to be the least affected by external conditions of any character that shows marked varietal differences. This character-complex is corolla size. The fact that corolla size is so comparatively constant under all conditions attending development has such a definite bearing on some broad questions of organography that it merits separate discussion. On this account, the liberty of asserting the truth of the statement with only the following data in its support is requested.

During the past four years, I have grown about 20 species of *Nicotiana* in considerable numbers. They have been grown under very diverse conditions. Some have been starved in four-inch pots, others have had the best of greenhouse treatment; some have had poor field conditions, others have had all field conditions practically at their best. The height of the plants, the size of the leaves, and similar size complexes have varied enormously, but the size of the corollas has scarcely varied at all. For example, plants of *Nicotiana silvestris* Speg. and Comes grown to maturity in four-inch pots produced no leaves longer than 7 in. On the other hand, sister plants of the same pure line produced leaves 30 in. long in the field. Both series, however, produced flowers with the same length and spread of corolla. Furthermore, cuttings from 20 of the field plants reported in this study were rooted and grown in small pots in the greenhouse. Their blossoms were the same size as those of the field grown plants from which they came.

The material used in this particular experiment consisted of pure lines of two *Nicotiana* types that are generally treated as distinct species (pl. VI). The male parent was *Nicotiana alata grandiflora* Comes, it being the plant called *Nicotiana affinis* by horticulturists. Three lots of it were under observation; one was obtained from Italy and the other two from the United States, but the original sources of the strains are unknown. These three lots were alike, and in successive generations were constant in their characters. They accorded perfectly with COMES' description and were remarkably narrow in their variability. The female parent I have called *Nicotiana forgetiana*, Hort. Sand., and thereby hangs a tale. I found in the Gray Herbarium of Harvard University a sheet from near Los Angeles, California, marked *Nicotiana clevelandii* Gray.

This designation was manifestly incorrect, as the plant was exactly like SANDER'S figure of *N. forgetiana* in the *Botanical Magazine* (No. 8006). As it had been collected only a few years, I took seed from one of the capsules and planted it. It grew and again produced plants like *N. forgetiana*. Miss DAY, the librarian of the Gray Herbarium, then looked up the correspondence regarding the specimen and found that it was evidently a garden specimen grown by a Californian botanist, since deceased, from seed furnished by Sander & Sons and called *N. Sandarae*. The plants have not the mixed colors and the variability of the specimens now sold as *Sandarae* hybrids, but are constant in their characters and are identical with *Nicotiana forgetiana*. I have come to the conclusion, therefore, that I have obtained (as LOCK[2] probably did) seeds of the real *N. forgetiana* that had been mixed with the *Sandarae*[3] hybrids by Sander & Sons.

In view of the fact that *N. alata grandiflora* and *N. forgetiana* do not differ essentially in their foliage and habit of growth, but only in flower size and color—the one being white, the other red—perhaps one should not call them two species. I hold no brief either way. I simply accept the taxonomic ruling. At least, there existed here two strains very different from each other and very constant in their characters. Both were self-fertile, and in fact were usually self-pollinated naturally. They were crossed. There was no trouble about this, as every cross attempted was successful, and the capsules were filled with seeds.

This, then, seemed to be an excellent opportunity for studying size inheritance: two strains, uniform in pure lines, one with a corolla three times the length of the other, could be crossed easily. All was not plain sailing, however, for the plants of the F_1 generation (pl. VII) were absolutely self-sterile. This fact would have cut off the experiment in the flower of a promising youth but for the further fact that each plant was perfectly cross-fertile with every other plant. It did indeed reduce my interest in the inheritance of corolla size, for it precluded the study of an F_3 generation, but this was offset by the more fascinating problem of self-sterility.

[2] Ann. Roy. Bot. Gard. Peradeniya 4: 195–227. 1909.

[3] The *Sandarae* hybrids were supposed to have been produced by the cross *N. forgetiana*×*N. alata grandiflora*.

It was impossible to study the F_3 generation because crosses between two F_2 individuals alike somatically would be without meaning, since nothing could be known of the gametic potentiality of each. Crosses between F_1 individuals, on the other hand, meant something, because they were alike gametically. Six F_1 crosses were made therefore, and from them were grown 828 plants.

TABLE I

FREQUENCY DISTRIBUTIONS FOR LENGTH OF COROLLA IN A CROSS BETWEEN *Nicotiana forgetiana* AND *N. alata grandiflora*

Designation	Class centers in millimeters														
	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90
N. forgetiana, 314	9	133	28	..	..	..	..	..	..	..	..	..	..	..	..
N. alata gr. 321	..	..	..	..	..	..	..	..	..	1	19	50	56	32	9
F_1 (314×321)	..	..	..	3	30	58	20	..	..	..	..	..	..	..	..
F_2 (314×321) 1–6	..	5	27	79	136	125	132	102	105	64	30	15	6	2	..

Table I shows the frequency distribution for length of corolla of *N. forgetiana* (314) inbred, *N. alata grandiflora* (321) inbred, the F_1 generation (314×321), and the F_2 generation (314×321) 1–6. The measurement was taken from the end of the pedicel to the center of the contraction commonly known as the corolla throat. The classes have a magnitude of 5 mm. and are centered at the even centimeters and half-centimeters. A glance at the distributions themselves is sufficient to show the small variability of the parent types and of the F_1 generation, and the great variability of the F_2 generation. The F_1 generation is strictly intermediate, as is the mean of the F_2 generation. *Among the individuals of the F_2 generation, however, are flowers identical with each parent.* This last fact is perhaps more clearly shown in the figures of pls. IX and X.

The statistical constants for each frequency distribution are shown in table II.

The spread of the corolla, measured to the tips of alternate lobes, behaved in the same way. Corolla breadth in *N. forgetiana* varied from 25–35 mm., with a sharp mode at 30 mm. The corolla spread of *N. alata grandiflora* was somewhat more variable in terms of the arithmetical standard, ranging from 55 mm. to 80 mm. The range of the F_1 individuals extended from 45 mm. to 55 mm.

In the F_2 generation plants were produced with a corolla breadth identical with each parent. In fact, there were four individuals as small as the smallest specimens of N. *forgetiana*, and there was one individual with flowers within 3 mm. of the size of those of the largest *N. alata grandiflora* growing in my cultures. The mean of this distribution was 48.57 ± 0.19 mm., the standard deviation 8.07 ± 0.13 mm., and the coefficient of variation 16.62 ± 0.28 per cent.

TABLE II

STATISTICAL CONSTANTS FOR FREQUENCY DISTRIBUTION OF TABLE I

Designation	Mean	Standard deviation	Coefficient of variation
N. forgetiana, 314	25.6 ± 0.12	2.27 ± 0.08	8.86 ± 0.33
N. alata gr., 321	78.8 ± 0.28	5.38 ± 0.20	6.82 ± 0.25
F_1 (314×321)	44.3 ± 0.23	3.67 ± 0.17	8.28 ± 0.38
F_2 (314×321) 1–6	49.9 ± 0.26	11.26 ± 0.19	22.57 ± 0.39

Examination of the F_2 generation of this cross indicated a correlation between the length of the corollas and the lengths of the filaments and the styles that for all practical purposes was perfect. By this statement I mean that the anthers were invariably just above the stigmas and the stigmas were invariably at the throat of the corolla. Of course absolute measurements would not show an integral coefficient of correlation, nevertheless one may assume, I think, that the fact is simply obscured by slight fluctuations. It seems as if the numbers were adequate from which to conclude either that the determiner or determiners of corolla length are also determiners of the length of the style and the filament or that these factor complexes are perfectly coupled in inheritance.

Corolla spread is also correlated with corolla length. It is by no means uncommon to find a sharp break in the correlation, as is witnessed by the individual with the very broad corolla and comparatively short tube pictured in pl. X, fig. 8; but one never finds inverse extremes in the same individual. Just what the correlation coefficient $0.610 \pm .015$ would prove to mean if individual analysis of later generations were made, is doubtful. We cannot go back of the gross statement that such a correlation exists

in the general population. Perfect coupling of certain factors together with independent combination of others may be possible; partial coupling arising from a peculiar gametic distribution may be equally possible.

TABLE III

CORRELATION BETWEEN LENGTH AND SPREAD OF COROLLA IN F_2 GENERATION OF CROSS BETWEEN *N. forgetiana* AND *N. alata grandiflora*

Breadth of corolla in millimeters

Length of corolla in millimeters	25	30	35	40	45	50	55	60	65	70	75	
25	1	...	4	...	...	...	...	...	...	...	...	5
30	2	5	4	10	3	3	...	...	...	...	...	27
35	1	5	17	26	21	6	3	...	...	...	...	79
40	...	6	12	38	41	31	7	1	...	...	...	136
45	...	...	8	20	29	31	26	8	2	1	...	125
50	...	...	3	22	30	44	25	7	1	...	...	132
55	...	...	1	2	22	27	37	9	4	...	...	102
60	...	...	1	3	11	32	29	19	9	1	...	105
65	...	...	...	...	6	17	21	12	7	1	...	64
70	...	...	...	1	1	5	15	4	4	...	...	30
75	...	...	...	...	...	7	3	4	...	1	...	15
80	...	...	...	...	...	1	1	3	...	...	1	6
85	...	...	...	...	...	1	...	...	1	...	...	2
	4	16	50	122	164	205	167	67	28	4	1	828

Coef. cor. 0.610 ± 0.015

These are the principal facts collected regarding this cross, if the small leaf differences and other minor variations are left out of consideration. How unimportant the latter are, can be seen by a reference to pl. VIII. There are several suggestions that may be made regarding the simple facts obtained, however, that may be helpful in further Mendelian interpretations of size complexes.

Elsewhere[4] it has been shown that the behavior of such characters in crosses is adequately represented by the segregation and

[4] Amer. Nat. **44**:65–82. 1910.

recombination of cumulative unit factors that do not show the phenomenon of dominance. The frequency distribution of the F_2 generation in these cases is not $(\frac{3}{4}+\frac{1}{4})^n$, as it is where dominance is complete, but is $(\frac{1}{2}+\frac{1}{2})^{2n}$, because a factor in the heterozygous condition is to be regarded as producing one-half the effect that it produces when in the homozygous condition.

Regarding this expression as proper for the moment, let us examine the F_2 frequency distribution for length of corolla with the idea of assigning a definite number for n in the expression $(\frac{1}{2}+\frac{1}{2})^{2n}$.

If n is made equal to 3, then by the theory the F_2 distribution should have seven classes with the frequencies

1–6–15–20–15–6–1

per 64 individuals. For 828 individuals, the grandparental sizes should each be recovered $(828 \div 64) = 13.0-)$ nearly thirteen times. This was not the case in the actual distribution.

If n is made equal to 5, the F_2 distribution should have eleven classes with the frequencies

1–10–45–120–210–252–210–120–45–10–1

per 1024 individuals. With 828 individuals the grandparental classes should each be recovered only 0.8 times; in fact, a majority of populations of this size would not show the grandparental classes at all. This also is not the condition that was actually found.

There is left only the possibility of making n equal to 4. When this is done the F_2 distribution for 256 individuals—the smallest number in which a representative of each class may be found—and for 828 individuals is as follows:

1 – 8 – 28– 56– 70– 56– 28– 8– 1
3.2–25.9–90.6–181.1–226.4–181.1–90.6–25.9–3.2

This calculation points to the recovery of each grandparent about 3 times in the F_2 population under observation. Reference to table I shows that the figures actually obtained agree rather closely with this observation. But table I also shows another important fact. The arbitrary classes used had a range of 5 mm., which makes 13 classes necessary to express the F_2 generation.

This class size was adopted in accordance with the usual biometrical procedure, the variations in the small parent (314) being included in only 3 classes. But when this is done, the F_2 distribution is decidedly skew. The theoretical mode is along about the fourth or fifth class instead of the central class. What is the reason for the production of this type of curve? There must be a reason, and it seems to me that this reason must be biological and not a mathematical transnomination, as have been all the biometrical analyses of skew curves. The matter appears clear in the light of the following interpretation.

In ordinary statistical work, one produces a frequency distribution by throwing his tabular entries into arbitrary classes of equal size. By this procedure he has in all probability distorted their relationship. This fact is partially recognized by using the coefficient of variability instead of the standard deviation as a measure of variation. Unfortunately, it is usually said that the coefficient of variability is used instead of the standard deviation because it is an abstract measure and pounds can be compared with inches, etc. Standard deviations in the same concrete terms are usually thought comparable with each other. But is this true? Apply the rule to the data in tables I and II. The range of length of corolla of *N. forgetiana* (314) is 3 classes, the standard deviation is 2.27 ± 0.08 mm., and the coefficient of variability is 8.86 ± 0.33 per cent. The range of *N. alata grandiflora* (321) is 6 classes, its standard deviation is 5.38 ± 0.20 mm., and its coefficient of variability is 6.82 ± 0.25 per cent. Comparing standard deviations, *N. alata grandiflora* is twice as variable as *N. forgetiana*. Comparing coefficients of variability, which being functions of the mean give weight to the size of the mean, the large-flowered type (321) is less variable than the small-flowered type (314).

Let us now look at the matter from an ordinary common-sense biological standpoint. These pure line populations may be considered as composed of near-homozygous individuals. The range of variability shown is therefore almost wholly due to environment. In general, *N. alata grandiflora* has a corolla more than twice as long as *N. forgetiana*. Is it not reasonable to suppose that the unit change effected by environment and expressed as a

fluctuation is proportional to the size of the individual? Is it not true that favorable circumstances which force the corollas of *N. forgetiana* to become 5 mm. longer than usual will produce a 10 mm. change in *N. alata grandiflora?*

If this is the correct way of looking at these two cases, then it is assuredly an error to plot the F_2 distribution—which includes both grandparental sizes—in classes of equal size. Assuming that our hypothetical size factors affect the individual as growth forces, it seems probable that they are not only cumulative but accelerative. Roughly one might imagine the effect on the individual to be something like a constant percentage. I do not believe these cases of size inheritance can be analyzed into their component factors and these factors given their proper weight (using the word factor in the general sense of elements or causes that produce a result) sufficiently well to give a precise value to the character determiners themselves. On the other hand, it is interesting to see just what is necessary in the way of class range to bring our F_2 corolla distribution to the normal distribution for four factors ($n=4$). Fortunately the corolla sizes were taken by millimeters, so this can be done. First I have smoothed the figures according to the regular method. The distribution in one-millimeter classes is then as follows (table IV, p. 186).

Suppose now we begin at 24 mm. and take for this class a range of 4 mm. Then let us increase our class range 1 mm. each time. This gives a simple arithmetical progression with an advancing difference of the second order, that is, the differences between the class ranges are constant. Compare the frequency distribution thus obtained with the expansion of $(\frac{1}{2}+\frac{1}{2})^{2n}$ where n is equal to 4. This is done in table V, with an agreement among the figures that is very remarkable. If I were a biometrician, I probably could show that this agreement could not be due to chance—since by chance it could only occur once in some hundreds of thousands of times—and must therefore have some great significance. I should prefer to believe that I happened by chance upon a series of class ranges that fitted the normal frequency theory. But it must be emphasized that it was a *constant* increase in class range that produced the normal curve from the distorted skew curve.

Perhaps no two actual frequency distributions would be alike in thus yielding to a simple arithmetical correction. Such a correction is probably fallacious in its simplicity. It serves our purpose,

TABLE IV

MEASUREMENTS OF LENGTH OF COROLLA IN F_2 POPULATION OF CROSS BETWEEN *Nicotiana forgetiana* AND *N. alata grandiflora*

Size mm.	freq.	Size mm.	freq.	Size mm.	freq.
24	0	45	25	66	12
25	2	46	28	67	10
26	2	47	29	68	7
27	2	48	28	69	7
28	1	49	28	70	6
29	3	50	26	71	6
30	5	51	28	72	5
31	8	52	23	73	6
32	10	53	20	74	4
33	11	54	20	75	3
34	15	55	19	76	2
35	13	56	22	77	2
36	18	57	22	78	0
37	18	58	22	79	1
38	19	59	26	80	2
39	26	60	21	81	2
40	28	61	22	82	1
41	33	62	15	83	0
42	24	63	15	84	1
43	23	64	14	85	0
44	24	65	12	86	1

TABLE V

COMPARISON BETWEEN THE THEORETICAL FREQUENCY DISTRIBUTION FOR FOUR FACTORS AND THE ACTUAL FREQUENCY DISTRIBUTION RESULTING WHEN CLASSES WITH A CERTAIN CONSTANTLY INCREASING RANGE ARE USED

Class limits	24–27	28–32	33–38	39–45	46–53	54–62	63–72	73–83	84–95
Class range.....	4	5	6	7	8	9	10	11	12
Frequency.....	6	27	94	183	210	189	94	23	2
Calculated frequency for 828 individuals for $(\frac{1}{2}+\frac{1}{2})^8$.....	3.2	25.9	90.6	181.1	264.4	181.1	90.6	25.9	3.2

however, if it calls attention to the manifest error of expressing a wide range of biological variation by a frequency polygon of equal size classes.

Summary

Concluding, the following points may be again emphasized:

1. The inheritance of size complexes is so intricate that it is necessary to simplify an experiment upon them in every possible manner. The material used in this investigation, *Nicotiana forgetiana* Hort. Sand. and *N. alata grandiflora* Comes, lacks three of the complicating features that usually ensnarl such work. They are almost always naturally self-fertilized, and through numerous generations of self-fertilization have become automatically as homozygous in their characters as may be expected in plants that reproduce sexually. Their fecundity is so great that practically any quantity of F_2 individuals can be produced from a single F_1 plant. A plant character was investigated upon which the effect of environment is so small as to be negligible, namely corolla size.

2. These self-fertile species, which are perfectly fertile *inter se*, gave self-sterile progeny. This fact did not affect the production of an F_2 generation, as the F_1 plants from homozygous parents are alike in gametic constitution, and these were perfectly fertile *inter se*.

3. *N. forgetiana* with a mean corolla length of 25.6 mm. crossed with *N. alata grandiflora* with a mean corolla length of 78.8 mm. resulted in an intermediate F_1 generation with a mean variability of 44.3 mm.

4. The variability of the F_1 generation was very small, being about the same as that of the remarkably constant parental species. The F_2 generation, on the contrary, was very variable and both grandparental types were reproduced.

5. It is shown that the F_2 generation is what would be expected if the difference in corolla length shown by these two species were represented by the segregation and recombination of four cumulative but independent pairs of unit factors, dominance being absent.

6. The coincidence of theory and result is as great in this case as it is in qualitative characters of like complexity. If the Mendelian notation is useful to describe complex qualitative inheritance, it is similarly useful in describing the inheritance of quantitative characters.

7. Length of style and of filament are perfectly correlated with corolla length.

8. Breadth of corolla shows an average correlation with length of corolla equal to 61 per cent.

9. The frequency distribution of corolla length for the F_2 generation is positively skew. It is pointed out that the range of fluctuations of corolla length in the two pure species is twice as great in the one of larger size than in the other. Classes of equal size in frequency distributions of great variability appear to be arbitrary and improper, if size factors are assumed to be dynamic factors with fluctuations roughly expressed by the term growth force. To show this accelerative action, the class ranges must gradually increase as the size (that is, the number of factors) increases. It is shown that the distribution under discussion will be changed from skew to normal if a simple arithmetical increase in the size of the classes is made.

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EXPLANATION OF PLATES

PLATE VI

At the left, a young flowering plant of *Nicotiana alata* Link and Otto, var. *grandiflora* Comes; at the right, a young flowering plant of *N. forgetiana* Hort. Sand.

PLATE VII

A mature plant of the first hybrid generation of a cross between *N. forgetiana* and *N. alata grandiflora*.

PLATE VIII

Figs. 1, 2, and 3, upper, median, and lower leaves of a mature plant of *N. alata grandiflora;* figs. 4, 5, and 6, upper, median, and lower leaves of the first generation of a cross between *N. forgetiana* and *N. alata grandiflora;* figs. 7, 8, and 9, upper, median, and lower leaves of a mature plant of *N. forgetiana*.

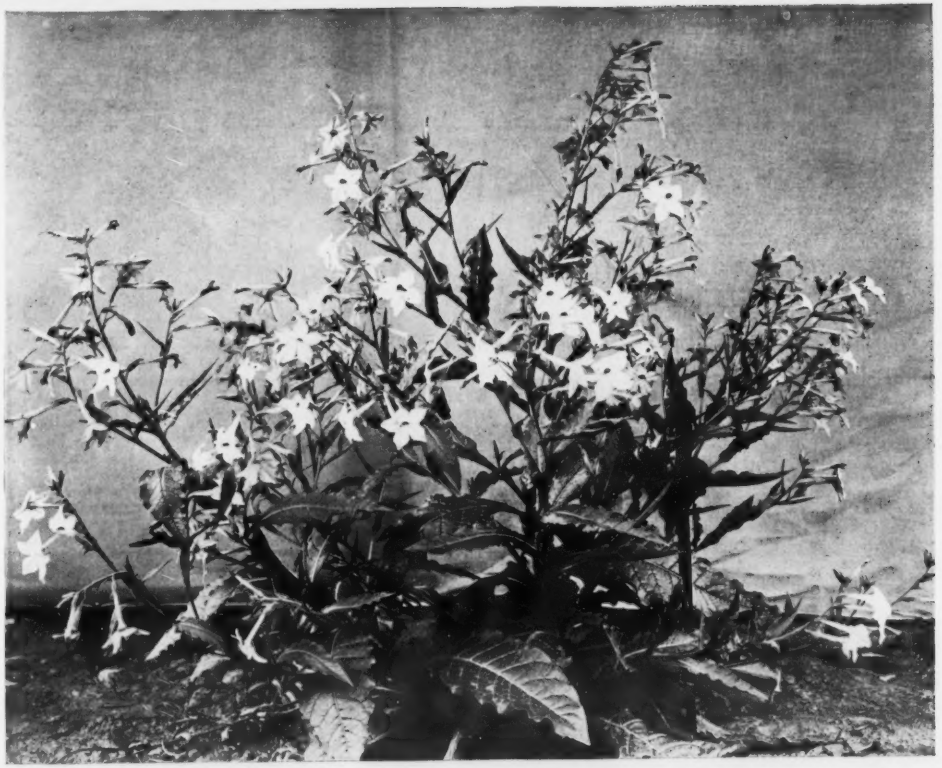
PLATE IX

At the left, a flower of *N. alata grandiflora;* at the right, a flower of *N. forgetiana;* between them are extreme F_2 segregates in length and spread of corolla; taken on the same plate, three-fourths natural size.

PLATE X

Fig. 1, *N. alata grandiflora;* fig. 2, *N. forgetiana;* fig. 3, cross between *N. forgetiana* and *N. alata grandiflora*, F_1 generation; the remaining figures are F_2 segregates; all figures are three-fourths natural size.

EAST on NICOTIANA



EAST on NICOTIANA

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THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. III

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 165

WILLIAM S. COOPER

(WITH TWENTY-FIVE FIGURES)

The hydrarch successions

The bog succession

I. Physiographic development of the bog habitat

At the commencement of the glacial period the topography and the drainage system of what is now Isle Royale were very similar to those of today, except that lakes and swamps were few or absent. This topography was but slightly modified by the invasion of the ice, and the most important change effected by glacial erosion was the excavation of rock basins in the preglacial valleys. Since the retreat of the ice the gradual emergence of the island from the waters of the lake has taken place. In some cases inclosed basins appeared above the surface ready made; in others they were produced by wave-built bars thrown across the mouths of harbors or both ends of channels during pauses in the retreat of the waters. By continued emergence some of these rock basins and cut-off bays came to occupy positions far in the interior of the island. The tilting which followed the Lake Nipissing stage must have had some effect upon the island lakes thus formed. It may have brought about the partial draining of some, the enlargement and perhaps even origination of others, and occasional shifting of outlets; in all cases it must have produced a tendency toward migration to the southwest.

The physiographic development of the bog habitat thus includes as a rule two periods: first, the channel-bay stage, and second, the lake stage. Numerous localities that illustrate the process may be seen today, especially at the northeast end of the island. Duncan

Bay would become a lake if the water level should sink 5–6 m.; Pickerel Cove is a similar case; and the inland portion of Rock Harbor is nearly closed at its narrowest point by a sand bar that has been built almost to the surface.

Several of the lakes of Isle Royale are of respectable size. Siskowit Lake, the largest, is more than 10 km. long and 2.5 km. wide (fig. 31). The majority are small, many being mere ponds.

All the lakes, and the harbors as well, are tending toward extinction through down-cutting of outlets, sedimentation, and vegetation. Down-cutting of outlets has as yet accomplished very

FIG. 31.—Siskowit Lake: the largest of the Isle Royale lakes

little. The large lakes like Siskowit are being filled by sedimentation with extreme slowness, because of the small size of the streams, their slight gradient, and the thick covering of vegetation which almost inhibits erosion of the land surfaces. It is impossible for bog vegetation to obtain a foothold in the large lake basins except here and there in very sheltered spots, because of vigorous wave and ice action (HOLT **33**, p. 218). They will therefore remain much as they are for a long time. In the small lakes, on the other hand, where wave and ice action are not severe, invasion by bog vegetation is in active progress.

II. Vegetational development in the bog habitat

1. Channel-bay stage

Even as early as the channel-bay stage we find the beginnings of the vegetational history of the bog habitat. If the body of water be large or subject to considerable wave and current action, plant life is practically absent. In sheltered places, however, there lives a plant society, sparse but characteristic. The commonest species is *Isoetes macrospora* Dur. (quillwort), growing entirely submerged at a depth of 0.3–1 m. in the silty sediment that covers the bottom. *Isoetes* here attains an unusual size, the crowns being frequently 5 cm. and more in diameter. With it grow occasional plants of *Chara* (stonewort), *Ranunculus aquatilis* L. var. *capillaceus* DC (water crowfoot), *Potamogeton perfoliatus* L. and other spp. (pondweeds). On shoals and along the reefs at the ends of the narrow islands and points are frequent clumps of sedges: *Carex aquatilis* Wahlenb., *C. stricta* Lam., *C. lenticularis* Michx.

2. Lake stage

The lake stage is considered as extending from the first complete inclosure of the body of water to the time when the bog vegetation has brought about its extinction. During this physiographic stage all the vegetational stages of the bog succession usually appear in their accustomed order. The aquatics are already present and the sedge society has often made a slight beginning. The latter now develops with rapidity, especially in the smaller lakes, and is followed in turn by the sphagnum-shrub society and the bog forest.

a) Peat formation

Peat formation in the northern and southern peninsulas of Michigan has been described by TRANSEAU (**56**) and by DAVIS (**19**). The bogs which DAVIS studied, especially in the Upper Peninsula, are very similar to those of Isle Royale, and this author shows that the sedge mat is the most important agent in the formation of the peat. Lack of time and facilities prevented a study of the basin-filling process upon Isle Royale, but it is certain that the bulk of the peat is deposited through the formation and sinking of the sedge mat and the accumulation of finely divided material

dropped from it. A subordinate amount is formed from the remains of the aquatic vegetation preceding the sedges in the invasion of the basins and from the shrub-sphagnum vegetation which follows them.

b) Illustrative localities

To illustrate the course of the bog succession upon Isle Royale several representative localities will be briefly described. Amygdaloid Lake shows the bog plants gaining their first foothold along the shore; the two ponds near Tobin's Harbor have been partially

FIG. 32.—Amygdaloid Lake: in the foreground a thick growth of *Menyanthes* and *Lysimachia thyrsiflora;* farther out, *Nymphaea advena.*

covered and filled; and the basin on Raspberry Island contains a completely covered bog.

Amygdaloid Lake (fig. 32).—Amygdaloid Island lies parallel to the northwest shore of Isle Royale and is formed by two partially submerged ridges of the usual kind. Between the ridges is an inclosed basin which contains a narrow lake, 100 m. wide at the most, but 1.2 km. long. It should be noted that Amygdaloid Lake is identically like the basin on Raspberry Island, to be described later, in situation and physiographic development. For some reason its history has not progressed so far, although both are at

the present lake level. It may be that the basin has been more recently shut off from Lake Superior than that on Raspberry Island, and also the depression is larger and doubtless deeper. The climax forest descends to the edge of the interior lake, except for an occasional short strip of stony or sandy beach. At the southwest end there is a considerable amount of bog vegetation, growing in water a few centimeters deep and underlain by 2 m. of soft mud containing much organic material. The principal aquatic is *Nymphaea advena* Ait. (yellow pond lily). There is next a zone of amphibious plants dominated by *Menyanthes trifoliata* L. (buckbean), which is accompanied by *Lysimachia thyrsiflora* L. (bog loosestrife) and a few other species. As will be noted later, *Menyanthes* is frequently an important mat-former. Through the middle of this zone winds a narrow streamlike ribbon of water, probably the last remnant of a sluggish outlet. Back of the *Menyanthes* zone and filling the continuation of the basin for 0.5 km. is the bog forest, composed of *Larix* and *Picea mariana*, with *Alnus incana* (L.) Moench (hoary alder) in front.

The arrangement of the vegetation here illustrates a feature characteristic of the bog-filled depressions of Isle Royale. On account of the elongated form of the basins, the building out of the bog vegetation goes on much more rapidly at the ends of the lakes than along their sides, because of gentler slope. Theoretically, also, it should build out faster on the northwest side than on the southeast, since by reason of the rock structure the former slope is normally gentler than the latter. In a few cases notable difference was seen in the width of the sedge mat corresponding to the difference in slope, but usually the width of the zone on the two sides was about the same. Probably talus deposits, slope wash, and sediments of various kinds tend to lessen the slope of the southeast side, making it more or less equal to that of the other.

It has been stated that along the greater part of the lake shore the climax forest descends to the water's edge. At one point (a sandy stretch) bog vegetation was found to be obtaining its first foothold. Farthest out were scattering plants of *Nymphaea advena*. Close to shore grew scattered stools of *Carex filiformis* L. (bog sedge) and plants of *Eleocharis palustris* (L.) R. & S. (creeping

spike-rush) and *Equisetum fluviatile* L. (scouring rush). Here we have the very beginning of the sedge mat, *Carex filiformis* being the most important mat-builder in most of the Isle Royale bogs. Next came a nearly bare level sandy shore 1–3 m. wide, at the upper edge of which began a second belt of bog vegetation. A line of depauperate *Menyanthes* with rootstocks creeping out over the gravel formed the lowest portion. It is probable that there has been a slight recent change of level in Amygdaloid Lake and that the *Menyanthes* marks the height of the former water surface. Above the *Menyanthes* was an area peopled by a number of species belonging partly to the bog forest and partly to the climax forest. These are as follows: *Lycopodium annotinum* L. (stiff club moss), *Smilacina trifolia* (L.) Desf. (three-leaved Solomon's seal), *Chiogenes hispidula* (L.) T. & G. (snowberry), *Symplocarpus foetidus* (L.) Nutt. (skunk cabbage), *Coptis trifolia* (L.) Salisb. (goldthread), *Linnaea borealis* L. var. *americana* (Forbes) Rehder (twin-flower), *Pyrola secunda* L. (shin leaf), *Cornus canadensis* L. (bunch-berry), *Trientalis americana* (Pers.) Pursh (star-flower), *Maianthemum canadense* Desf. (two-leaved Solomon's seal), *Mitella nuda* L. (mitrewort), *Moneses uniflora* (L.) Gray (one-flowered wintergreen).

This low vegetation was nearly smothered by a dense growth of sphagnum, much of it very young. The *Lycopodium*, which was the most abundant species of the list given above, showed only the tips of its branches except along the edge of the sphagnum mass, where thick clusters of new shoots projected from beneath the moss. The plants of *Coptis* were many of them buried up to the leaves. Upon the surface of the sphagnum grew *Drosera rotundifolia* L. (sundew) and *Linnaea*. A low beach ridge supported the most luxuriant sphagnum growth, which was occasionally as much as 0.3 m. deep, especially where it surrounded shrubs and tall grasses. *Calamagrostis canadensis* (Michx.) Beauv., *Agrostis hyemalis* (Walt.) BSP, *Iris versicolor* L., *Campanula uliginosa* Rydb. (bog bell-flower) grew here, and also *Alnus incana* (L.) Moench. (hoary alder). It is noteworthy that everywhere along the shore, except where the sphagnum has become established, *Alnus crispa* rather than *A. incana* forms the forest margin. In and around the sphagnum grew a few bog trees, *Larix* 1–3 m. in height, and young

Picea mariana and *Thuja;* and back of these was a narrow band of bog forest, hardly more than a single line of large trees, *Larix* and *Thuja*, with much young *Abies* and *Betula*, and the usual herbaceous growth of such a habitat, practically the list given above. The sphagnum was evidently spreading from the ridge both toward the water and into this area of bog forest. Behind all was the climax forest of balsam, spruce, and birch.

It is evident from the foregoing description that at this locality we have in embryo every society or zone of the bog succession,

FIG. 33.—Sucker Lake: aquatics; sedge zone of *Carex filiformis* type, fringed with *Menyanthes;* at the left a narrow zone of shrubs and a thin line of tamaracks bordering the climax forest; a thick growth of bog trees at the end of the basin (distance).

from the aquatics through the sedge mat (represented by the stools of *Carex* and its companions), the sphagnum-shrub zone supporting the nascent bog forest, to the mature bog forest invaded by the climax trees; and all in the space of only 10 m. It is thus demonstrated that all the zones may begin their development at approximately the same time.

Sucker Lake (fig. 33; Sec. 34, T. 67 N., R. 33 W.).—The development of the bog vegetation is here far advanced. A wide zone of aquatics nearly surrounds the small area of open water, and this in turn is surrounded on three sides by a broad sedge mat made up of

Carex filiformis L., *C. limosa* L., *C. chordorrhiza* L. f., *C. polygama* Schkuhr, *C. oligosperma* Michx., and *C. livida* (Wahlenb.) Willd. Along the outer edge of the mat and almost forming a zone by itself is a fringe of *Menyanthes*, its thick rootstocks closely intertwined. The shrub zone, dominantly *Myrica Gale* L. (sweet gale), is poorly developed, and sphagnum is nearly absent, only a sparse growth being seen and this nearly choked by the luxuriant sedges. Along much of the southeast shore the sedge mat is absent and the shrubs are the marginal vegetation. Here *Chamaedaphne* and

FIG. 34.—Pond near Tobin's Harbor in Sec. 5, T. 66 N., R. 33 W.: aquatics occupying center; sedge zone of *Carex filiformis* type; in the background hoary alder and tamaracks bordering the climax forest.

Andromeda grow actually in the water. DAVIS (**19**) has noted this replacement of the sedge zone by a shrub mat as a very common occurrence in the bogs of the northern peninsula of Michigan, but it is rare on Isle Royale. The bog forest at Sucker Lake is a mere line of tamaracks along the sides of the basin, but is well developed at both ends, where great stretches of the narrow depression have been converted into a forested valley. Sucker Lake is the last remnant of a body of water that was once very similar to the Rock Harbor of today.

Pond near Tobin's Harbor (fig. 34; Sec. 5, T. 66 N., R. 33 W.).—This locality is closely similar to the last and occupies the same type of basin, with considerable bog forest at both ends. Development has proceeded one step farther, there being no open water, and the aquatics thus occupy the center. The sedge zone is continuous and everywhere equally developed. Soundings through the mat showed that the slopes of the bottom on the northwest and southeast sides are not notably different. *Carex filiformis* is the principal mat-former. The other species contributing are *Carex*

FIG. 35.—Same locality as fig. 34: *Scirpus hudsonianus* prominent in the sedge zone: islands of shrubs, *Alnus incana* surrounded by *Chamaedaphne;* a thick growth of bog trees at the end of the basin.

limosa L., *C. chordorrhiza* L. f., *C. Michauxiana* Boechl., *C. livida* (Wahlenb.) Willd., and *C. polygama* Schkuhr. The principal bog herbs accompanying the sedges are as follows: *Menyanthes trifoliata* L. (buckbean), *Potentilla palustris* (L.) Scop. (marsh cinquefoil), *Vaccinium Oxycoccos* L. var. *intermedium* Gray (cranberry), *Rhynchospora alba* (L.) Vahl (white beak-rush), *Cicuta bulbifera* L. (water hemlock), *Hypericum virginicum* L. (marsh St. Johnswort), *Scirpus hudsonianus* (Michx.) Fernald (alpine cotton-grass), *Epilobium palustre* L. (marsh willow-herb), *Scutellaria galericulata*

L. (skull-cap), *Lysimachia terrestris* (L.) BSP (loosestrife), *Campanula uliginosa* Rydb. (bog bell-flower), *Galium Claytoni* Michx. (bedstraw), *Lycopus uniflorus* Michx. (bugle-weed), *Sarracenia purpurea* L. (pitcher-plant), *Drosera rotundifolia* L. (round-leaved sundew), *Iris versicolor* L., *Arethusa bulbosa* L., *Spiranthes Romanzoffiana* Cham. (lady's tresses), *Habenaria dilatata* (Pursh) Gray (white bog orchis), *H. psycodes* (L.) Sw. (purple-fringed orchis). *Sphagnum* is rare. The shrub zone is better developed than at Sucker Lake and includes two subzones: the outer, in which *Chamaedaphne calyculata* (L.) Moench is dominant and accompanied by *Andromeda glaucophylla* Link and *Salix pedicellaris* Pursh; the inner, of *Alnus incana* (L.) Moench. Advance islands of shrubs are scattered here and there over the sedge mat, the outermost being composed of *Chamaedaphne*, and the inner of a nucleus of *Alnus incana* surrounded by a circular zone of *Chamaedaphne* (fig. 35). Seedlings of tamarack are frequent in these colonies. The subzone of *Alnus incana* fringes the outer edge of the bog forest, which here as usual is a mere line along the sides, but broader at the ends. The bog tree is the tamarack.

3. Open bog stage: Raspberry Island bog

Raspberry Island is one of the row that bounds Rock Harbor on the southeast, and is next in line to Smithwick Island, studied in connection with the climax forest. Its upland forest cover was originally like that of Smithwick, but unfortunately this has been largely fire-swept, the bog area, however, having escaped unharmed. The island consists of two parallel ridges of the typical Isle Royale kind, bounding a narrow depression, closed at both ends by beach ridges, which contains the bog area. The outer ridge is the more massive of the two and makes the bulk of the island, while the inner is only half as long. Both reach an elevation of about 10 m. The island has emerged from the lake in comparatively recent time, and its history has been a simple one; moreover it is in all essentials the history of Isle Royale itself on a small scale. When the lake level was 3 m. higher than now there was a channel over the site of the bog area. At this time currents and waves were doubtless at work building bars across the channel mouths. With continued sub-

sidence of the lake level the bar at the exposed southwest end emerged and became a beach connecting the two ridges, which now inclosed a sheltered bay. Into this considerable sediment was still being carried by waves and currents. As the lake level continued to fall, the more slowly building bar across the sheltered northeast end of the harbor emerged, and the bay was now an inland lake. It is probable that the height of both beaches has been increased since their emergence through the agency of storm waves. The physiographic history of the habitat is thus concluded. Its likeness to Amygdaloid Island will be at once evident. At Amygdaloid Lake we find the beginnings of the bog vegetation; Raspberry Island shows its culmination, in the sense that at this stage the open water has disappeared, and all the bog societies are present and at their best development. The further history will record the progressive extinction of these societies by centripetal invasion.

The relations of the zones to each other are shown in the

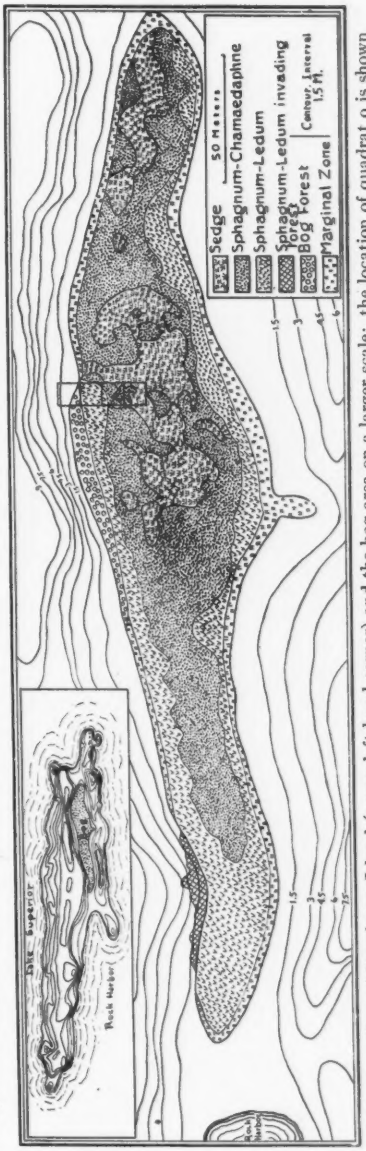

FIG. 36.—Map of Raspberry Island (upper left-hand corner) and the bog area on a larger scale: the location of quadrat 9 is shown

map (fig. 36) and in the general view (fig. 37). Certain features of the succession were so well developed in this bog that they must have a place in this account.

The sedge mat is composed almost entirely of *Carex limosa* L. (mud sedge) (fig. 38). Occasional bare muddy spots are nearly free of sedge, but support a scattered growth of *Menyanthes* and *Drosera anglica* Huds. (narrow-leaved sundew). These appear to represent the youngest stage now existing in this habitat.

FIG. 37.—Raspberry Island bog: general view; sedge zone of *Carex limosa* type in the foreground; the sphagnum-shrub society occupies most of the view; young bog trees as pioneers of the forest; black spruce prominent in the bog forest.

a) The sphagnum and its relations

Particular attention was given to the sphagnum, which is very luxuriant in this bog; especially to its point of origin, the conditions governing its spread, and its relations to companion species.

The first point to be noted is that the sphagnum is a superficial layer supported upon the sedge mat, and thus does not contribute in any large degree to peat formation. This feature has been noted by HOLT (**33**) for the Isle Royale bogs, and by TRANSEAU (**56**) and DAVIS (**19**) for the northern and southern peninsulas of Michigan.

The next important fact is that the sphagnum does not make its first growth at the extreme edge of the bog area and from here works its way centerward only. On the contrary, it begins its growth some distance within the bog margin and works both ways; very slowly toward the margin, faster toward the center. Proof of this course of events is seen in the entire absence of sphagnum from the marginal zone, except in certain parts where it is manifestly a recent invader. Soil samples taken at various depths in

FIG. 38.—Sedge zone of *Carex limosa* type; Raspberry Island

the marginal zone, examined microscopically, failed to show the slightest trace of sphagnum remains, although these are long preserved and readily recognized. Another proof is found in the form of the sphagnum accumulation, which is that of a ridge parallel to the bog margin and at a somewhat constant distance from it. This ridge usually has its greatest thickness close to the outer (marginal) side, doubtless marking here the region of first growth. It will be remembered too that in the primitive stage observed at Amygdaloid Lake the sphagnum was seen to be spreading both ways. The face toward the bog margin (on Raspberry Island) is usually rather abrupt, forming a prominent wall which bounds the marginal zone. Occasionally a thin layer of sphagnum is found

to be invading the latter area. In the opposite direction (centerward) the sphagnum decreases *gradually* in thickness, and at its edge invasion of the sedge zone is actively taking place. Fig. 39, drawn to scale, is a typical bog section. The form of the ridge is shown and also the depth at various points. The high projection upon the sphagnum mass is a hummock, the true marginal face being at the right. A tongue of the moss is seen invading the marginal zone. Below the line which is drawn as marking the base of the sphagnum the soil is black peat containing little that is recognizable even with a microscope. At several places, however, sphagnum fragments were recognized in various degrees of abundance some centimeters below the line indicated. These were

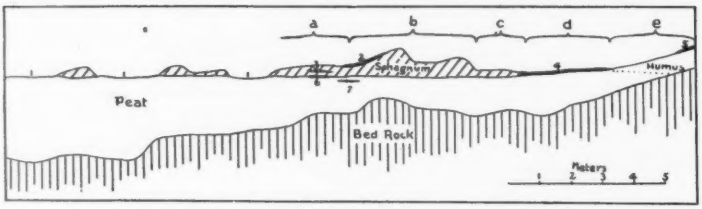

FIG. 39.—Section through Raspberry Island bog: *a*, *Sphagnum-Chamaedaphne; b*, *Sphagnum-Ledum; c*, *Sphagnum* invading marginal trench; *d*, marginal trench; *e*, upland; *1*, sedge zone; *2*, *Calliergon Schreberi; 3*, *Calliergon Schreberi* (fossils); *4*, *Carex trisperma* and *Hylocomium proliferum; 5*, *Hylocomium proliferum; 6*, *7*, *Drepanocladus vernicosus* (?) (fossils).

probably washed down from above, since this line certainly indicates the plane at which the growth began.

The development of the sphagnum has not made uninterrupted progress, for at *3* on the section a stratum was found which contained abundant fragments of *Calliergon Schreberi*, and at *6* and *7* remains of *Drepanocladus vernicosus* (Lindb.) Warnst. were discovered. These two species evidently obtained a foothold upon the surface of the sphagnum and for a time arrested its growth over certain areas. The latter again gained the upper hand and buried the invaders.

The zone included between the sphagnum and the slopes of the upland commonly takes the form of a circular trench. This "marginal trench" is a widespread feature of bogs, and various

causes for its occurrence have been suggested by MACMILLAN (38), SHAW (52), DAVIS (19), and ATKINSON (5). None of these explanations could be applied with certainty to the phenomenon as observed upon Isle Royale, but that offered by ATKINSON seemed most plausible, that is, that during the early development of the sedge mat the sphagnum was excluded by the shade cast by the near-by forest growth. Only after the bog substratum had built out beyond the shaded area did the moss become established upon it.

FIG. 40.—Tension zone between sedge and sphagnum-shrub societies: *Carex limosa* and *Chamaedaphne* keep pace with the growth of the sphagnum by upward elongation; Raspberry Island.

The third point to be considered is the manner of invasion by the sphagnum, including its relations to the sedges and other plants which it finally replaces, and to the shrubs which accompany or follow it. The sphagnum area spreads marginally, and at the same time colonies of young plants originate among the sedges in advance of the main mass. Several such colonies are shown on the map (fig. 36). By the coalescence of these and the solid mass behind, the sphagnum zone extends itself at the expense of the sedge mat.

Certain plants of the sedge zone persist for some time after the sphagnum has gained control. They do this by a process of upward

elongation, keeping pace in this way with the building up of the moss. *Carex limosa* itself survives for a considerable time. Stalks of this species apparently growing on the sphagnum can always be traced down to the stratum beneath, and the buried portions are found to be covered with dead remnants of leaves (fig. 40). *Menyanthes* manages to persist for a time in a similar way. *Sarracenia*, which as a rule precedes the sphagnum, makes use of the same method in an endeavor to hold its own, but is less successful

FIG. 41.—Zonal arrangement of bog shrubs: *Andromeda* in the foreground, mainly upon the sedge mat; *Chamaedaphne* (middle ground at the right) mainly upon a mound of sphagnum; Raspberry Island.

and is soon buried. Certain of the bog shrubs belong to the same class. *Chamaedaphne*, *Andromeda*, and *Salix pedicellaris* usually precede the sphagnum. When the moss starts its growth in the vicinity of these plants it builds up rapidly around their stems, forming the hummocks that are so characteristic of sphagnum bogs. Of the three shrubs, *Chamaedaphne* has the greatest power of holding its own against the smothering tendency of the moss (fig. 40); the willow is next; while *Andromeda* soon succumbs.

The two important bog shrubs, *Andromeda* and *Chamaedaphne*, are zonally arranged (fig. 41). *Andromeda* grows freely on the sedge mat, especially in the wetter parts, is most abundant just at the

edge of the sphagnum, and occurs to a limited extent some distance back in the moss. *Chamaedaphne* is also found commonly upon the sedge mat, but inhabits the drier portions. In the sphagnum area it is abundant and over a wide belt almost the only shrub, extending back until it meets the zone where *Ledum groenlandicum* is the dominant species. Relative ability to withstand extreme wet bog soil conditions determines this zonation at the beginning, but the sudden elimination of *Andromeda*, leaving *Chamaedaphne* in full control, is due principally to the smothering effect of the sphagnum, which the former shrub is unable to avoid. *Chamaedaphne*, on the other hand, is able to grow up with the moss indefinitely, and therefore persists until the entrance of *Ledum* introduces a new factor. It is not certain that *Chamaedaphne* does not sometimes germinate upon the surface of the sphagnum as well as upon the sedge mat, and thus in part maintain its dominance. It is certain, however, that *Andromeda* does not commonly do so, at least not successfully. Two other shrubs, *Kalmia polifolia* Wang (pale laurel) and *Betula pumila* L. (dwarf birch), occur in this and other bogs, but not in sufficient abundance for satisfactory study of their habits.

Upon the surface of the sphagnum another group of species becomes established. Important among these are *Carex pauciflora* Lightf., *Smilacina trifolia* (L.) Desf. (three-leaved Solomon's seal), *Drosera rotundifolia* L. (round-leaved sundew), *Vaccinium Oxycoccos* L. (small cranberry). All of these are able in greater or less degree to keep pace with the continued upward growth of the moss.

Of far greater importance than these is *Ledum groenlandicum* Oeder (Labrador tea), which becomes established long after the other shrubs, indeed after all but *Chamaedaphne*, have disappeared. *Ledum* is almost invariably found to be related definitely to the sphagnum, its whole root system being contained within the mass. The growth that it forms is very dense (fig. 42), and as it is a taller shrub than *Chamaedaphne* it shades it severely, and thus finally causes its elimination. Its effect upon the sphagnum is similar. Because of the shade which *Ledum* produces and the considerable amount of waste which falls from it, the upward growth of the moss is gradually retarded and finally ceases altogether.

About this time or often before, young plants of other mosses more or less tolerant of shade become established upon the higher parts of the sphagnum mass. *Polytrichum strictum* Banks is the first arrival, and *Aulacomnium palustre* (L.) Schwaegr. and *Calliergon Schreberi* (Willd.) Grout soon follow. These species form mats of continually increasing lateral extent, which put an effectual stop to further upward growth of sphagnum.

FIG. 42.—*Sphagnum-Ledum* zone, the moss entirely concealed by the abundant growth of the latter; the edge of the bog forest in the background; Raspberry Island.

b) Sphagnum invading the forest

The fact has been mentioned that the sphagnum frequently spreads into the marginal zone as well as toward the center of the bog. In some places this invasion is so effective that the marginal zone is entirely obliterated. The moss does not always stop even here, but occasionally climbs entirely out of the bog, invading the climax forest. A case of this kind was reported by HOLT (**33**) from a locality near Siskowit Lake. A far more striking instance was discovered on Raspberry Island, near the northeast end of the bog (see map, fig. 36 and fig. 43). In a stretch of 50 m. along the margin the sphagnum had completely obliterated the marginal zone and had ascended the slope for varying distances. At the point of

farthest advance the mass had taken the form of a tongue 4 m. wide, extending 10 m. from the true bog margin. The slope of its surface was about 25° and the highest point reached was 4.5 m. above the bog level. The sphagnum supported a luxuriant growth of *Ledum* which completely covered it. The unusual abundance of flowers in comparison with the plants of the bog itself was a noteworthy feature, as was also the comparatively small size of the leaves, both facts perhaps indicating somewhat hard conditions. *Vaccinium Oxycoccos* and *Chiogenes hispidula* were also abundant, and frequent small seedlings of birch, black spruce, and balsam were found. The depth of the moss was 0.6–1 m., and the edges were abrupt, but unfortunately the fire which destroyed the upland forest had encroached somewhat upon the bog vegetation, so that the marginal conditions could not be ascertained.

FIG. 43.—*Sphagnum-Ledum* society invading the upland forest: the view is taken from the bog, and shows the bog vegetation climbing the slope to a height of 4.5 m.; Raspberry Island.

4. The bog forest and its development

Although in the Raspberry Island locality the bog forest is not so extensively developed as in other places, all the essential features are present. A series of four adjoining units was laid out, each 5 m. square, the whole forming a broad section cutting through all the societies from the sedge zone to the climax forest (quadrat 9, fig. 44). The manner of invasion of the sedge mat by the sphagnum is shown. To avoid confusion the distribution of the bog shrubs is indicated only in a general way. The trees of the various species, their locations, and ages are given in the manner made use

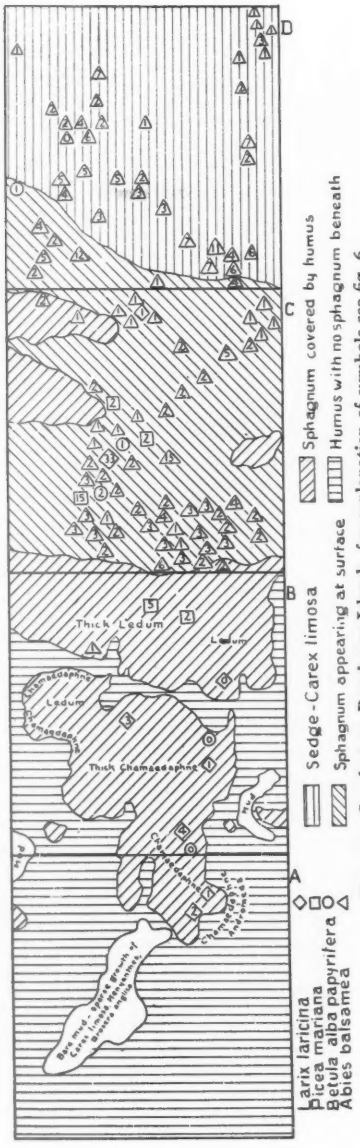

FIG. 44.—Quadrat 9: Raspberry Island; for explanation of symbols see fig. 6

of in the charts of the climax forest.

The most important fact to be obtained from the diagram is that in no part of the section is there anything approaching pure bog forest. In quadrats *A* and *B* there is a mere scattering of invaders; *C* and *D* are occupied by a young climax forest growth with a few bog trees, most of which are relicts. The absence of pure bog forest is due to the fact that the trees of the climax stage follow immediately after the first invading bog trees, or even accompany them. In accordance with the usual habit of the species, balsam seedlings germinate in enormous numbers, and although many of them succumb to the stress of competition, they shade the ground so that no more bog trees, which are light-requiring species, can start. The climax trees, *Abies*, *Betula*, and *Picea canadensis*, having come into possession are able to hold their ground in the manner described in an earlier section of this paper. The further history merely records the gradual dying out of the bog relicts.

Though there is little *pure* bog forest upon Isle Royale, there is abundance of a very characteristic type which may be called "impure" bog forest; that is, forest composed of a mixture of bog and climax trees. Upon Raspberry Island it is poorly developed,

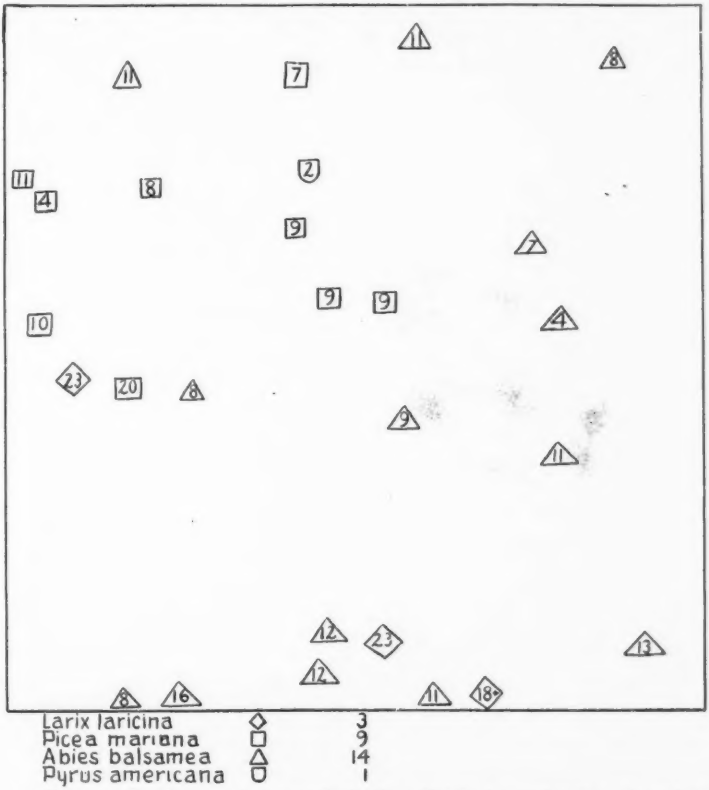

FIG. 45.—Quadrat 10: bog near Park Place Hotel; for explanation of symbols see fig. 6.

but there is an excellent sample near the Park Place Hotel on Rock Harbor (Sec. 3, T. 66 N., R. 33 W.). A quadrat in this locality was studied and the results are shown in fig. 45. The oldest trees here were the three tamaracks, and they were also much the largest, being 2.75–5.25 dm. thick, and towering above their companions.

One of them was hollow, and all were more or less attacked by rot. The black spruces were found to be somewhat younger than the tamaracks. All were solid to the heart. The balsams, which were most numerous of the tree species, were of various ages from 47 to 161 years. No young balsams were present and the average age was very high (105 years). All showed signs of suppression during early life, probably due to shading by the faster growing bog trees. Within the last half-century the tops have reached the sunlight, and most of the balsams are now growing rapidly, though many are rotten hearted, as is common with this species. Two birches close to the quadrat, 1.5 dm. and 2.25 dm. in diameter, were found to be 62 and 69 years old respectively. No white spruce occurred in this locality, but the species is present in most areas of bog forest. A striking fact is the absence of reproduction (fig. 46). No tree younger than 47 years was seen except a few one or two-year-old seedlings of birch and mountain ash, which seem able to germinate in deep shade but not to continue growth.

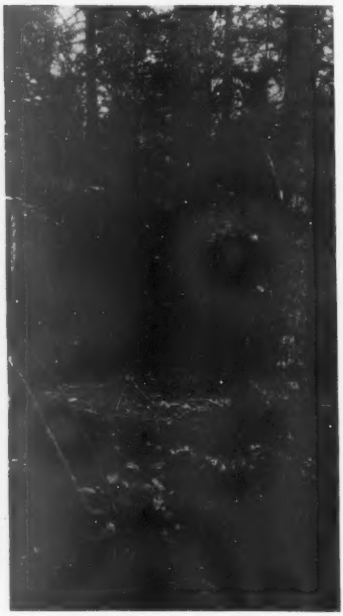

FIG. 46.—Bog forest interior; locality of quadrat 10: two large tamaracks in the background; black spruce, balsam, and *Alnus incana;* carpet of *Carex trisperma* with *Petasites* and other species; note absence of tree reproduction.

The history of the area is probably as follows. The present generation of trees of both bog and climax type started during the period of open bog conditions, and growing up together produced so dense a shade as to inhibit the starting of new growth beneath them. Shelter from wind, due to the depression in which they grow, is doubtless the reason for the absence of windfalls and the unusually long life of the balsams. No reproduction will take

place until light is admitted to the forest floor by the destruction of some of the present generation.

The characteristic bog forest shrubs are the alders. *Alnus incana* is found principally near the bogward edge, while *Alnus crispa*, belonging rather to the climax forest, inhabits the landward portions.

In the lower vegetation mosses are most prominent both in quantity and variety; 22 species were taken from a single area of bog forest. *Sphagnum* spp. (relicts of the open bog stage), *Calliergon Schreberi* (Willd.) Grout, and *Hylocomium proliferum* (L.) Lindb. make up the bulk of the moss carpet. Sharing the forest floor with these is *Carex trisperma* Dewey which, accompanied by *C. leptalea* Wahlenb. and *C. tenella* Schkuhr, forms dense green mats of considerable size. In some places *Lycopodium annotinum* L. covers the ground, and in others there is a rank growth of *Equisetum sylvaticum* L. As minor features there are certain herbs that particularly characterize the bog forest. The most numerous are *Habenaria obtusata* (Pursh) Richards, *Listera cordata* (L.) R. Br., *Smilacina trifolia* (L.) Desf., *Phegopteris Dryopteris* (L.) Fée, *Mitella nuda* L., *Coptis trifolia* (L.) Salisb., *Viola incognita* Brainerd, *Petasites palmatus* (Ait.) Gray.

The outstanding feature in the later part of the bog succession is the telescoping of stages. The sphagnum-shrub stage (when present) is hardly well established before the bog trees enter, and immediately following them or often actually with them come the climax trees. The reason for the early establishment of the latter is found in the likeness between the bog soils and those of the forested uplands. Those of the uplands are nearly as peaty in texture and properties as are those of the bogs. The causes of the peatiness of the upland soils trace back to other factors: low evaporation rate due to low temperatures; poor drainage because of solid rock substratum; and probable paucity of certain types of bacterial and fungal life. It follows, the two soils being much alike, that whatever trees can grow upon one may exist also upon the other.

5. Two types of bogs

One of the numerous questions that could not be settled with entire satisfaction related to two fairly distinct types of bogs

involving somewhat different courses of succession. One had an abundant growth of sphagnum associated with much *Ledum*, and *Picea mariana* and *Larix* composing the bog forest. Those of the other type had little sphagnum, often practically none, and in these *Ledum* was rare or absent and *Picea mariana* almost never found, the bog trees being *Larix* and *Thuja* or *Larix* alone. The Raspberry Island bog is an excellent example of the first, which we may designate the sphagnum type; and Sucker Lake and the other pond near Tobin's Harbor illustrate the second, or sedge type. In some cases these types may represent stages in the same succession, since sphagnum often does not become dominant until late in the history of a bog, and *Ledum* and *Picea mariana* follow the sphagnum, being dependent upon its presence. But it is certain that in many cases the *Sphagnum-Ledum* stage is entirely eliminated, and that when this happens *Picea mariana* does not appear, or holds a very subordinate place in the bog forest. The succession in such cases is as follows: (1) aquatics, (2) sedge mat, (3) shrub zone (*Chamaedaphne*, *Andromeda*, *Alnus incana*), (4) bog forest (*Larix*, often with *Thuja*). It is obvious that *Sphagnum* is the critical plant, since *Ledum* and *Picea mariana* come later and only in bogs where the moss is abundant.

Certain differences were noted in the conditions prevailing in the two types of bogs. It was universally true in the sphagnum bogs that were visited that the drainage was poor or lacking, the only water loss being due to very slow seepage and evaporation. Those of the sedge type on the contrary were usually well drained. There was often open water in the center, in which case the bog might well be at a stage earlier than that of sphagnum dominance. The covered bogs without much sphagnum usually possessed one or more small streams flowing in and an active outlet. In a few cases, however, the drainage was seemingly as poor as in the sphagnum bogs. As to the way in which these drainage differences affect the vegetation, if they do affect it, nothing was determined.

Another fact was noted which quite certainly has a bearing upon the presence or absence of sphagnum. It was found that the sedge mat is composed of different species in the two types of bogs. In the sphagnum bogs *Carex limosa*, a low, soft, loosely growing

stoloniferous species, was usually the principal mat-former, and *Menyanthes*, with somewhat similar characteristics, was next in importance (compare figs. 33 and 38). In those of the sedge type, tall stiff sedges growing in dense clumps were most important, forming a thick meadow-like growth. *Carex filiformis* was the commonest species, but certain areas were found to be dominated by *Scirpus caespitosus* L., the most densely tufted of all the sedges. These two kinds of sedge mat form very different substrata for the growth of the sphagnum. On account of the shortness and softness of *Carex limosa* the moss is never seriously shaded where that sedge is dominant, and it is able to grow over and around the *Carex* and *Menyanthes* plants and thus to spread laterally with ease. The sedges in this case offer no effective resistance, and the sphagnum soon gains the ascendancy over them. Where *Carex filiformis* and plants of similar habit are the principal mat-formers the moss, if it starts among the closely placed clumps, is shaded from the beginning. It cannot spread laterally among the dense clusters of thick culms, and so remains in a half-smothered condition until exterminated through the advance of the shrubs and trees. The distribution of the two kinds of mat-forming plants still remains to be accounted for, and for this I have as yet no explanation. It is entirely possible that the type of sedge which gains the dominant place in a given bog may be determined merely by accidental causes.

FIG. 47.—Bog forest in well drained portion of a bog near Siskowit Lake: *Larix* and *Alnus incana*.

Occasionally the two phases may be seen in a single bog. For

instance, in a locality near Siskowit Lake (Sec. 32, T. 65 N., R. 35 W.) the central area (which is better drained than the rest, having a sluggish stream meandering through it) is of the sedge type. Some patches of bog forest near the stream are made up almost entirely of *Larix*, with much *Alnus incana* as undergrowth. In the poorly drained areas near the margin the forest is pure *Picea mariana*, and the ground is carpeted with solid sphagnum covered with an abundant growth of *Ledum*. These two phases are shown in figs. 47 and 48.

FIG. 48.—Bog forest in poorly drained area; same locality as fig. 47; *Picea mariana*, *Ledum*, and *Sphagnum*.

The delta swamp succession

I. Extent and distribution

The delta swamp succession comprises the successive stages of vegetational development which culminate in the establishment of the climax forest upon the deltas and alluvial plains of the streams. These societies do not occupy an extensive area in the aggregate, but they are exceedingly interesting because of the close interdependence between the successional and the physiographic processes. Delta swamps of various sizes are found at the heads of most of the bays, and are probably present also where streams of any size enter the larger lakes. Protection from the waves and currents of Lake Superior is naturally essential to their development. The localities studied were as follows: head of McCargoe's Cove (Sec. 26, T. 66 N., R. 35 W.), Brady Cove (Sec. 18, T. 66 N., R. 35 W.), Duncan Bay (Sec. 6, T. 66 N., R. 33 W.), Lake Richie outlet at Chippewa Harbor (Sec. 18, T. 65 N., R. 34 W.), Hay Bay (Sec.

24, T. 64 N., R. 37 W.), head of Siskowit Bay (Sec. 33, T. 64 N., R. 37 W.).

II. Physiographic development of the habitat

The history of the present deltas began with the initiation of stream activity as the island emerged from the lake. The amount of erosion accomplished by the streams of Isle Royale has been very slight. The sources of the materials transported by them have been principally two: the products of wave erosion left high and dry as the lake level sank, and weathered rock material, including some decomposed by organic agencies. Deposits were made at the mouths of the streams at all stages during the emergence of the island. As the lake surface sank these were transported to successively lower levels, and more materials were added. Of course some of the earlier deposits may have been so situated as to have escaped removal, but no such remnants have been reported. It is therefore probable that the present deltas include most of the materials that made up the earlier ones, brought down from level to level as the streams were repeatedly rejuvenated by successive sinkings of the lake surface.

Delta building seems to have practically ceased, at least temporarily, for three reasons: (1) the available loose material accumulated during the successive stages has all been brought down and deposited; (2) the complete forest covering of the uplands practically inhibits further weathering and erosion, except what may be accomplished by the slow organic processes; (3) (applicable only to northeastward-flowing streams, which, however, are in the majority) tilting has taken place in the Lake Superior region since the formation of the Nipissing beach (ADAMS 4). At Isle Royale the elevation of this beach is about 18 m., and it rises northward to 27 m. at Nipigon. This has decreased the gradient of northeastward-flowing streams and thus has tended to reduce their erosive and transporting power.

The result of these processes has been the formation of flat delta plains of gravel, sand, and silt at the heads of many of the harbors, with streams, practically currentless, meandering over them. Cut-and-fill and scour-and-fill are going on to some extent

in these streams, which processes are due principally to alternating currents produced by seiche movements (ADAMS 4) of the waters of Lake Superior. The currents thus produced are quite considerable. At one moment there is a strong outward flow; a few minutes later the movement may be just as swift in the opposite direction. The effect of the seiche current is practically the same as that of an ordinary stream current. It undermines the bank in some places and deposits the eroded materials in others. On account of its alternating direction the gradational effects in a particular case cannot be so simply worked out, but judging from the relative positions of the eroding and depositing portions of the banks it seems probable, as one would naturally expect, that the outward current is the more effective. It is possible that occasional heavy rains may considerably increase the volume and velocity of the streams. The channels are not ordinarily sunk far into the sedimentary substratum. Their banks appear largely as vertical sections of the layer of plant growth which has spread over the delta plain.

III. Vegetational development in the habitat

The first vegetation upon the delta deposits enters when the water over them shallows sufficiently to permit the growth of aquatics of the pondweed type. Next come water lilies and rushes, and when the sediments accumulate until they reach nearly to the surface, sedges gain a foothold and soon form a mat. Up to this point the development has followed the same course as the bog succession. Important differences now appear. The sedge mat does not build out over the water, probably because of wave and ice action, since the bodies of water into which the streams flow are rather large and open. The sedge mat stage does not last long, but is very soon superseded by a dense growth of tall grasses, among which *Calamagrostis canadensis* (Michx.) Beauv. is by far the most important. It is this type of plant, growing in dense, closely placed stools, that forms the bulk of the stratum of plant remains which finally covers the plain. The grasses are followed by shrubs, and these by the swamp trees, which finally give way to the climax forest.

Among the delta swamps studied, the largest was at the head of McCargoe's Cove. The alluvial flat was here 0.8 km. long by 0.4 km. wide. All the stages are here well developed except the swamp forest, which has been fire-swept. Part of the meadow-like marsh is shown in fig. 49, and a sketch map of the delta is given in fig. 50. Farthest out, in water a meter and more deep, is a zone of *Potamogeton perfoliatus* L. Within this, in a few inches of water, grows *Equisetum fluviatile* L. Next comes the sedge mat, firmly grounded, with *Carex filiformis* as the principal species, accompanied

FIG. 49.—Delta swamp at the head of McCargoe's Cove: sedge, grass, and shrub societies are shown; the swamp forest has been burned.

by bog herbs. The area dominated by *Calamagrostis* is the most extensive, and its level is perceptibly higher than that of the sedge zone. With *Calamagrostis* grow other herbaceous species, many of them tall, such as *Thalictrum dasycarpum* Fisch. and Lall. (tall meadow rue), *Chelone glabra* L. (turtle-head), *Epilobium angustifolium* L. (fireweed), and *Symplocarpus foetidus* (L.) Nutt. (skunk cabbage). Stools and patches of *Calamagrostis* were seen as invaders of the sedge society, and occasional shrubs, pioneers of the next group, were scattered over the area occupied by the grass.

Myrica Gale L. (sweet gale) is the first shrub to invade the

meadow swamp. It is followed by *Alnus incana*, which at first is pure, but farther back is found mixed with other shrubs: *Cornus stolonifera* Michx. (red osier dogwood) and *Viburnum pauciflorum* Raf. (high bush cranberry). With these come the invaders from the forest, *Fraxinus nigra* Marsh (black ash) being usually the first arrival. Burned stumps indicate that there was once an extensive development of swamp forest along the east side of the delta, in which *Thuja* was the important tree.

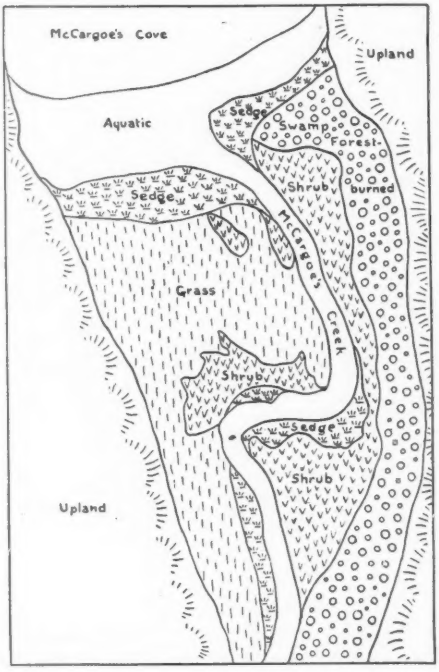

FIG. 50.—Sketch map of the delta at the head of McCargoe's Cove.

The stream which winds through the swamp is 6–10 m. wide and 0.3–1 m. deep. Its channel is constantly changing by reason of its own undermining and depositional activity. Near the outer edge of the marsh it crosses the belt of sedges. Farther back it is bordered by various societies. Where it cuts into the grass-covered areas erosion by undermining is going on, and a section of peat sometimes 0.6 m. in height is exposed. For considerable distances shrubs are also being undermined, and at one point the stream in its meandering has invaded the area of former swamp forest and has caused the overthrow of many trees. The material eroded from the banks is deposited where the current slackens, and in such places the normal succession of plant stages is in progress; aquatics first, followed by a sedge mat when the

deposit reaches the surface. Frequently the first invaders are stools of sedge or rootstocks of *Nymphaea* and *Calla* which have been washed out from some eroding portion of the shore.

It may thus be seen how the plant life supplements the physiographic processes. Upon one bank the current may be steadily destroying the vegetation (grasses, shrubs, and even trees); while on the other, where deposition is in progress, the same types are being developed through the normal course of the swamp succession.

Note should be made of the peculiarly rich aquatic flora which inhabits the shallows of this and similar sluggish streams. The list of species obtained in the several localities of this type includes the following of special interest: *Nymphaea advena* Ait., *Vallisneria spiralis* L., *Utricularia vulgaris* L. var. *americana* Gray, *U. intermedia* Hayne, *U. minor* L., *Myriophyllum verticillatum* L. var. *pectinatum* Wallr., *M. spicatum* L., *M. alterniflorum* DC, *Potamogeton natans* L., *P. alpinus* Balbis, *P. amplifolius* Tuckerm., *P. heterophyllus* Schreb., *P. heterophyllus* f. *terrestris* Schlecht., *P. praelongus* Wulf., *P. perfoliatus* L., *P. zosterifolius* Schumacher, *P. obtusifolius* Mertens and Koch, *P. filiformis* Pers., *Callitriche palustris* L., *Castalia tetragona* (Georgi) Lawson, *Bidens Beckii* Torr., *Scirpus subterminalis* Torr., *Sparganium diversifolium* Graebner, *S. minimum* Fries, *Sagittaria latifolia* Willd. f. *hastata* (Pursh) Robinson, *S. cuneata* Sheldon, *Lemna trisulca* L., *Ceratophyllum demersum* L., *Hippuris vulgaris* L., *Glyceria borealis* (Nash) Batchelder, *Calla palustris* L., *Isoetes macrospora* Dur. Though not a plant, *Spongilla* should be mentioned as an important element in the aquatic life.

At the head of Duncan Bay there are two delta swamps, both smaller than the one just described. One of these was studied with care, and the locality is included here because the swamp forest is well developed. *Fraxinus nigra* is the pioneer, and is present, but not abundant, in the mature forest. *Thuja* comes next and is the most important species. *Larix*, *Picea canadensis*, *Abies*, and *Betula alba* var. *papyrifera*, in order of abundance as named, complete the list. In passing toward the shoreward edge of the swamp forest *Larix* is the first to disappear. *Thuja* holds out much longer, and the ground is covered in places with tangles of layered branches

from it. The young trees are largely balsams. The herbaceous growth is practically the same that is found in the bog forest. It will be noted that all the trees of the climax forest are present here, and that the stages are telescoped as in the bog succession.

A locality where the climax condition had been almost attained was found in a narrow stream valley at the head of Brady Cove (Sec. 18, T. 66. N., R. 35 W.). The forest here, which fills the valley, is of the climax type except for an occasional ancient *Thuja* and a slight admixture of *Fraxinus nigra*. Fallen trunks of *Thuja* are fairly numerous. The shrubs and herbs are a mixture of swamp forest and climax forest species.

That there is a general resemblance between the bog succession and the delta swamp succession is very evident. There are also some striking differences which are constant in the localities studied. Most important of these are the following: sedge mat not floating; interpolation of grass stage as the most important peat-forming agency; absence of sphagnum, true bog shrubs, and *Picea mariana;* dominance of *Thuja* in the swamp forest.

It is conceivable that under certain circumstances one succession might pass over into the other. This seems to have happened at the head of Siskowit Bay just north of Senter Point. A large swampy area has been cut off from the bay by a high curving beach ridge 1 km. long. That there was originally a delta swamp here is shown by the presence of a remnant of the former stream, a winding strip of water ending abruptly against the outer ridge. For some reason, possibly on account of post-Nipissing tilting, the current of the stream became insufficient to keep its outlet open in opposition to the vigorous wave action upon the shore of the bay. The resulting stagnancy has brought about a partial change to bog conditions. The former stream is partly filled with an open growth of *Menyanthes*, *Equisetum fluviatile*, *Utricularia intermedia*, and *Potamogeton heterophyllus*. Along the water's edge there is a band of nearly pure *Carex filiformis*, recently established. The body of the swamp is occupied by a sedge-grass society, in which *Scirpus caespitosus* is dominant. Accompanying species are *Carex exilis* Dewey, *Muhlenbergia racemosa* (Michx.) BSP, *Sarracenia purpurea* L., *Vaccinium Oxycoccos* L., *Aster umbellatus* Mill. var. *pubens*

Gray, *Solidago uliginosa* Nutt. Shrubs are scattered over the whole area, the principal species being *Potentilla fruticosa* L. and *Myrica Gale* L. The bog forest is of considerable extent and the trees are *Thuja*, *Larix*, and *Picea mariana*. Near the forest edge there is considerable sphagnum in hummocks much overgrown with grasses and other plants. The composite character of the vegetation in this locality is plain. It is certain that the change from swamp to bog conditions has been very gradual, and it is possible also that there has always existed here a slight element of bog vegetation.

THE SECONDARY SUCCESSION

The burn succession

I. Causes and extent of fires upon Isle Royale

During the period of mining activity upon Isle Royale fires were of frequent occurrence and many square kilometers were swept by them. Since the abandonment of the mines they have been much less frequent, so that most of the burned areas found today have already gone through a considerable period of forestward development. There is evidence that fires occurred long before the appearance of white men. A layer of burned wood deeply buried was found in the humus upon Smithwick Island, where otherwise absolutely no sign of burning was to be seen. Such fires must have been started either by Indians or by lightning. It is nearly certain that fire has played a part in the vegetational history of almost all if not the entire forested area of the island.

II. Effect of fire upon the climax forest

The effect of the destruction wrought by a forest fire is essentially to bring about a return to a more or less xerophytic condition, which is followed by a readvance leading again to the climax forest. The secondary development may be along the line of the original primary succession, but factors are usually present which bring about pronounced modifications in the process. Obviously the burn succession is exceedingly variable, and cannot be described in terms that will even approximately fit every case. The variable factor that is most important in creating differences in the succession is the severity of the fire. In respect to this two cases may be roughly distinguished.

1. *Humus little harmed.*—This is the commonest type of burn upon Isle Royale and results in the development of a characteristic "burn forest" preceding the reestablishment of the climax. The composition of such a forest is mainly the outcome of the differing success with which the various species withstand the effects of the

FIG. 51.—Recently burned area on Smithwick Island: fireweeds dominant; a relict birch at the left; unburned forest in the background.

FIG. 52.—Young birch stump sprouts in a two-year-old burn near Siskowit Lake.

fire. The coniferous element of the climax forest, consisting of *Abies balsamea* and *Picea canadensis*, is entirely eliminated by a fire of any severity. *Betula alba* var. *papyrifera*, on account of its dry papery bark, is very inflammable, and the aerial portions are quickly destroyed. The underground parts, however, are not killed as are those of the conifers. They persist with great tenacity through most unfavorable conditions, provided the humus in which

they are buried is unharmed, and are the most important contributors to the forest which immediately begins its development. *Pyrus americana* is similar to the birch in this respect, but is much less abundant. The shrubs of the climax forest seldom survive, though occasionally in a moist hollow a clump of *Taxus* will persist. The plants of the forest undergrowth, being close to the damp ground, frequently live through the fire. Some of them quickly succumb to the hard conditions which ensue, but certain species seem to thrive better than ever after the destruction of the forest cover. Prominent among the latter class are *Cornus canadensis*, *Linnaea borealis* var. *americana*, and *Maianthemum canadense*. These, which usually grow rather sparsely in the shade of the climax trees, come to cover large areas, flowering and fruiting luxuriantly. The first is one of the most characteristic species in the undergrowth of the burn forest.

Upon areas where the forest has been destroyed but the humus little harmed the progress of the burn succession is commonly as follows. During the first growing season after the fire those relicts which have survived renew their growth, and many new arrivals appear. Certain of the latter are much the most prominent features for a number of years. These are the familiar fireweeds, *Epilobium angustifolium* L. and *Anaphalis margaritacea* (L.) B. & H. (fig. 51).

Although the fireweeds give tone to the landscape for the first few years, the trees of the future forest begin their development equally early. The birches of the original stand, whose subterranean parts are still alive, sprout luxuriantly from the stump (figs. 52, 53). Often a ring of a dozen or more shoots appears where a single birch of the previous generation stood. Many of these die, but some develop into trees. Seedling birches and aspens (*Populus tremuloides*) add to the number, but upon Isle Royale the birch sprouts greatly predominate. The result is the development of a forest composed mainly of even-aged birches in clumps of 2–6 or more (fig. 54). A rich shrubby vegetation accompanies the trees. *Rubus idaeus* var. *aculeatissimus* is usually the first. *Diervilla Lonicera* Mill, *Corylus rostrata* Ait., and *Rubus parviflorus* Nutt. follow. When the birches have attained a size sufficient to produce

moderate shade, the last named shrub (white-flowered raspberry) often forms a dense tall thicket growth beneath them. There is also a characteristic group of herbs that follow close upon the decline of the fireweeds. These are *Castilleja pallida* (L.) Spreng. var. *septentrionalis* (Lindl.) Gray, *Lilium philadelphicum* L., *Pteris aquilina* L., and others in the early stages; and *Aster macrophyllus* L., very abundant in the mature burn forest. A forest mainly of birches in clumps, with undergrowth as described above, is practically certain indication that fire has recently visited the area.

FIG. 53.—A group of birch stump sprouts in an area that was burned about 35 years ago: the original trunk is shown; near Park Place Hotel.

Frequently neighboring burns of different ages are indicated by patches of birch forest of differing height.

None of the areas of burn forest of historic age upon Isle Royale are old enough to show the late stages in the transition to the climax. The process is indicated, however, by the frequent occurrence of young spruce and balsam under the light shade of the birches. Occasional conifers germinate immediately after the fire, but the thorough occupation of the ground by the fireweeds and the rapid growth of the birch sprouts, as well as the dryness of the ground, prevent them from starting in abundance. The devel-

opment of the burn forest is exceedingly rapid, thanks to the prolific sprouting of the birch, but the transition from burn forest to climax seems to be a slower process. Occasional areas of climax forest in which the birch element is mainly composed of groups of immense stump sprouts probably represent the penultimate stage in a burn succession following some prehistoric fire.

The effect of fire upon the composition of the flora is shown in table VI. The statistics were obtained from a study of areas of equal size in the unburned and burned portions of Smithwick

FIG. 54.—A young burned forest composed mainly of birches in clumps: the lower growth is *Juniperus communis* var. *depressa*, *Pteris aquilina*, and other species; near Park Place Hotel.

Island. The fire occurred about 15 years ago. The points to be noted are the destruction of the conifers and a part of the herbaceous flora, the increase of *Betula* and another portion of the herbaceous vegetation, and the appearance of *Populus*, *Rubus*, and the fireweeds.

2. *Humus destroyed; bare rock exposed.*—In such cases the reestablishment of the climax follows closely along the line of the rock shore succession, through lichen and crevice plant, and heath mat stages. Such differences as occur are due to the more thorough disintegration of the rock with greater abundance of soil materials

resulting therefrom; the presence of more or less humus at the beginning (it rarely happens that fire destroys every vestige of organic matter, and even a very small quantity in a rock crevice is of great assistance in hastening the establishment of vegetation); frequent protection from the drying and mechanical effects of wind;

TABLE VI

Species	Climax forest	Burn
Abies balsamea	65	1
Betula alba var. papyrifera	6	117 (sprouts)
Picea canadensis	1	...
Pyrus americana	13	...
Populus tremuloides	..	16
Taxus canadensis	14	...
Viburnum pauciflorum	1	1
Rubus idaeus var. aculeatissimus	..	74
Aralia nudicaulis	21	...
Mitella nuda	21	...
Trientalis americana	13	...
Linnaea borealis var. americana	6	30
Clintonia borealis	2	...
Epilobium angustifolium	..	806
Anaphalis margaritacea	..	421
Maianthemum canadense	*	312
Calamagrostis canadensis	..	83

* Frequent in most parts of climax forest.

presence of a large body of invaders ready to advance from all directions. All these modifying influences tend to hasten the progress of the succession. Areas where fire has exposed the bare rock are found principally upon the tops of ridges, since the soil in such places is usually both shallow and dry, and whatever remains after the fire is washed away to lower levels.

III. Effect of fire upon the xerophytic and bog forests

When the jack pine–black spruce forest is burned, much of the humus is apt to be destroyed also, as the soil is commonly thin and dry. A few observations indicate that this type often succeeds itself. The pine grows faster and so for a number of years is the dominant tree. In one burned locality was found an open growth of pines 4–7 m. high, even-aged, averaging 28 years. Beneath

them were scattered black spruces, few more than 1 m. high, also even-aged, and averaging more than a year older than the pines.

In extensive fires the patches of bog forest occupying the depressions often escape entirely because of abundant moisture. When they are burned over the coniferous element is destroyed, and the birches if present sprout from the stump. The underground portions of the two species of *Alnus* survive and renew growth, and the result is frequently a dense alder-birch thicket, which probably passes directly into the climax type. When the scattered trees growing upon an open bog are killed by fire the sphagnum, being usually saturated with water, seldom suffers severely. New bog trees begin growth and the succession goes on as before.

SUMMARY.—THE SUCCESSIONS

Primary successions

The xerarch successions

Every part of Isle Royale has at some point of its subaerial history been shore.

The present coast of the island is made up of rock shores and beaches, the former being much the more extensive. Each type possesses its characteristic series of successional stages, the ROCK SHORE SUCCESSION and the BEACH SUCCESSION, both resulting finally in the establishment of the climax forest.

With regard to area vegetated through its instrumentality, the rock shore succession is by far the most important of all the successions of Isle Royale.

The full series of the rock shore succession includes in its early stages three subsuccessions which later unite into a single series.

The *rock surface subsuccession* advances through crustose lichen and foliose lichen stages to a condition in which the large cladonias are the most important element. The process of invasion along this line alone is very slow.

The pioneers of the *crevice subsuccession* are certain herbs, notably *Potentilla tridentata*, whose principal rôle is the formation of humus. Trailing shrubs succeed them, the most important being *Juniperus horizontalis*, *J. communis* var. *depressa*, and *Arctostaphylos Uva-ursi*. These spread over the rocks from the

crevices in all directions, and weaving among the cladonias and plants of the rock pools bring about the formation of a firm mat. The crevice vegetation is of extreme importance because of its rapidity of development and its preeminent part in the formation of the heath mat. Forest establishment is accomplished much sooner where crevices are abundant in the rock than where they are scarce.

The *rock pool subsuccession* goes through its development in depressions where water stands at least a part of the time. These become gradually filled after the manner of the bog succession, and the vegetation later becomes an element in the formation of the heath mat.

The *heath mat* results from the coalescence of the vegetation developed through the instrumentality of the three subsuccessions named above.

The *climax forest* often follows immediately after the formation of the heath mat, the trees obtaining their first foothold in the crevices. A relatively xerophytic forest stage characterized by *Pinus Banksiana* and *Picea mariana* sometimes intervenes, in which *Pinus* is the pioneer and *Picea* remains for some time after the climax trees have attained dominance.

Telescoping of stages is pronounced throughout the series, so that pioneer and climax forms, with those of all intermediate stages, are frequently found occupying a single limited area.

The effect of special conditions upon the rock shore succession is expressed in the two following laws:

1. The lower limit of possible forest extension is determined approximately by the upper limit of effective wave and ice work, the lake level remaining constant.

2. The extent to which the forestable territory has been occupied at the present day depends upon the rapidity of invasion, which is governed by the character of the rock, the angle of slope, and the degree of exposure to winds.

The operation of these laws results in the production of three phases of rock shore vegetation, characterized respectively by (*A*) climax forest to the water's edge, (*B*) a zone of incomplete invasion, (*C*) abrupt transition from bare rock shore to climax forest.

During the early subaerial history of Isle Royale the rock shore succession may have differed from that of the present day. A study of Gull Islands indicates that birds may have been important agents in determining the composition of the primitive rock shore flora of the island.

The beaches on account of their sheltered location usually bear the climax forest down to its limit of possible extension. Low shrubs of various kinds are the most important pioneers in the beach succession, and larger ones, especially *Alnus crispa*, intervene before the establishment of the climax type.

The hydrarch successions

The bog succession

Physiographic development.—The depressions which now contain lakes or bogs owe their origin to glacial modification of the preglacial topography; sometimes to the cutting off of bays or channels by wave-built bars.

The physiographic history of the habitat in which the bog succession runs its course comprises two stages: the channel-bay stage and the lake stage. The lakes and harbors are tending toward extinction through the agencies of down-cutting of outlets, sedimentation, and vegetation, of which the last is the only one of importance at the present time. The lake stage ends when vegetation, aided by the other agencies, has entirely eliminated the open water.

Vegetational development.—During the channel-bay stage aquatics first appear and gradually increase with increasing shelter; the beginnings of the sedge mat are occasionally present.

During the physiographic lake stage all the vegetational stages of the succession appear in order: aquatics (usually already present), sedge mat, sphagnum-shrub, bog forest. All may have their beginnings at practically the same time. The sedge mat is usually the most prominent feature at this period. The sedges gain their first foothold in shallow water close to shore and build a floating mat out over the water. They are by far the most important agents in peat formation.

During the covered bog stage the plant societies are successively eliminated by the centripetal encroachment of the various zones.

Two lines of succession are distinguished after the sedge mat stage. One is characterized by *Chamaedaphne*, *Andromeda*, and *Alnus incana* in the shrub stage, practical absence of sphagnum, and by *Larix* and sometimes *Thuja* in the bog forest; the other by *Chamaedaphne* and *Andromeda* followed by *Ledum* in the shrub stage, abundance of sphagnum accompanying the shrubs, and by *Larix* and *Picea mariana* in the bog forest. Sphagnum is the critical plant in the differentiation of the two series, since *Ledum* and *Picea mariana* appear later, and only in cases where sphagnum is abundant. The differences may be related to differences in drainage, since those bogs containing little sphagnum are usually well drained, while in those with abundance of sphagnum, as far as observation has gone, drainage was very poor or lacking entirely. A contributing factor is found in differences in the composition of the sedge mat preceding the shrubs and sphagnum. In the sphagnum bogs *Carex limosa* is the principal mat-forming species. Being low and soft, it offers no resistance to the spread of the moss. In the bogs with little sphagnum *Carex filiformis* is the important mat-former. On account of its height and stiffness and dense growth it produces unfavorable conditions for the spread of sphagnum. The reason for the differing distribution of the two carices is unknown; it may be merely accidental.

The sphagnum is a superficial layer supported upon the sedge mat, and contributes little toward peat formation. It begins growth some distance within the bog margin and spreads both ways, slowly toward the margin, faster centerward. The area between the sphagnum and the upland commonly forms a marginal trench. In some places the moss by recent invasion has obliterated the marginal trench, and occasionally it transgresses the bog margin, spreading up the forest floor for several meters.

The sphagnum spreads marginally, surrounding and smothering such plants as cannot keep pace with its growth. Certain species by upward elongation are able to survive for some time, especially *Andromeda* and *Chamaedaphne*, the latter persisting longest.

Ledum almost invariably follows the sphagnum, and its root system is usually strictly confined to the masses of it. It forms a

very dense growth, and through its shading power and the great amount of waste that falls from it finally eliminates the lower shrubs and stops the upward growth of the moss.

The bog trees, *Larix*, *Thuja*, *Picea mariana*, usually follow the sphagnum when it is present. When it is lacking they start upon the sedge mat with the shrubs. The climax trees enter very soon after or often actually with the bog trees, so that pure bog forest is practically absent. The bog trees die out because they are intolerant of shading, and the climax forest results.

Telescoping of stages is prominent throughout the late history of the succession.

The reason for the early establishment of the climax forest is found in the likeness between the bog soils and those of the forested uplands, the latter being almost as peaty as those of the bogs. It follows that whatever trees can grow upon one soil may also exist upon the other.

The delta swamp succession

Delta deposits are found in most of the sheltered bays where streams enter from the upland.

The succession of vegetation upon these deposits passes through the following stages: (1) aquatics; (2) sedges; (3) grasses (*Calamagrostis canadensis* most important), which form broad meadow-like growths and produce a limited amount of peat; (4) shrubs, among which *Myrica Gale* and *Alnus incana* are most important; (5) swamp forest, made up of *Thuja occidentalis*, *Larix laricina*, and *Fraxinus nigra*, the first being dominant; (6) climax forest of *Abies balsamea*, *Betula alba* var. *papyrifera*, and *Picea canadensis*.

There is a general likeness to the bog succession; among other points, in the early establishment of the climax forest after the coming in of the swamp trees.

The important points of difference from the bog succession are: the firmly grounded sedge mat; interpolation of the grass stage; absence of sphagnum, bog shrubs, and *Picea mariana;* dominance of *Thuja* in the swamp forest.

Intermediate conditions between the two successions occur, and actual transition from delta swamp to bog succession occasionally takes place.

Secondary succession

The burn succession

The effect of fire upon the climax forest is to bring about a return to a more or less xerophytic condition, which is followed by a readvance leading to the climax. Two general cases may be distinguished.

1. *Humus little harmed.*—The coniferous element is destroyed, but the birches survive in their underground portions and sprout abundantly from the stump, usually producing a nearly pure

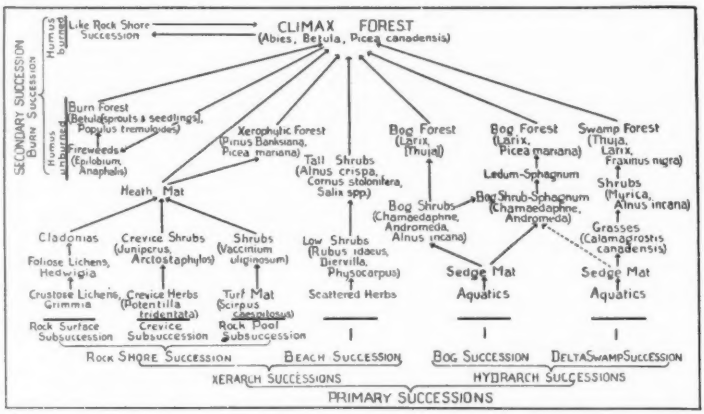

FIG. 55.—Diagram to illustrate the courses of the various successions upon Isle Royale.

forest of birches growing in clumps. Seedling birches and aspens are usually present also. Conifers gradually return, finally bringing about the reestablishment of the climax.

2. *Humus destroyed; bare rock exposed.*—The reestablishment of the climax follows closely along the line of the rock shore succession, but progress is usually more rapid because of the presence of soil materials and numerous invaders, and frequently protection from wind.

The courses of the various successions and their relations to each other are shown graphically in the diagram (fig. 55).

PALO ALTO, CALIFORNIA

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STUDIES ON THE PHLOEM OF THE DICOTYLEDONS

II. THE EVOLUTION OF THE SIEVE-TUBE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 169

ANSEL F. HEMENWAY

(WITH PLATE XI AND THREE FIGURES)

In 1909–10 the writer studied the phloem of some 30 species of lower dicotyledonous trees and found that the sieve-tubes in these species had the same general structure as those of the gymnosperms or vascular cryptogams.[1] Some 60 species of higher woody dicotyledons were investigated the next year, and this last year about 90 species of herbaceous dicotyledons and 12 monocotyledons have been studied.

As the literature on the subject of phloem has been rather well reviewed and catalogued recently, an exhaustive review of it will not be given here. In 1908 HILL[2] gave a good review of the literature from the histological standpoint. MANHAM[3] similarly discusses the literature from the physiological side. CHAUVEAUD[4] in an extensive paper gives a brief review of the literature of phloem.

The material for this investigation was collected in late summer or early fall, the object being to get the sieve-tubes in mature condition, so that they would best show callus formation. For the sake of comparison, several species were studied in seedling condition and in the adult growing condition.

Before proceeding to the discussion of the evolution of the sieve-tube, a few general observations on phloem anatomy may well be mentioned. The distribution of the hard bast in the woody

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[2] HILL, A. W., The histology of the sieve-tube of angiosperms. Ann. Botany **22**:245–290. *pls. 17, 18. figs. 13.* 1908.

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[4] CHAUVEAUD, G. L., L'appareil conducteur des plantes vasculaires et les phases principales de son évolution. Ann. Sci. Nat. Bot. IX. **13**:113–438. *figs. 218.* 1911.

dicotyledons is very characteristic for each species and usually for each genus. In many cases it is arranged in bands concentric with the cambium, as in *Acer*, *Populus*, and *Crataegus;* in some cases in groups opposite the large or aggregate rays, as in *Alnus*, *Carpinus*, and *Drimys;* in other cases in irregular patches, as in *Ostrya* and *Celtis;* and finally, in various combinations of these arrangements, as in *Quercus*.

Plate figs. 1–3 show some of these peculiarities of phloem structure. Fig. 1 is a transverse section of *Acer macrophyllum;* the lighter horizontal bands are the hard bast cells; between these are the sieve-tubes and parenchyma cells; while the dark vertical lines are the phloem rays; in the lower portion of the figure the cambium and some xylem are seen. Fig. 2 is a similar view of *Alnus incana;* here we note that the hard bast occurs chiefly opposite the aggregate ray. Fig. 3 is a similar view of *Quercus Garryana;* a large group of hard bast is seen above the large ray in the lower left portion of the figure, while several smaller groups appear here and there in other parts of the phloem.

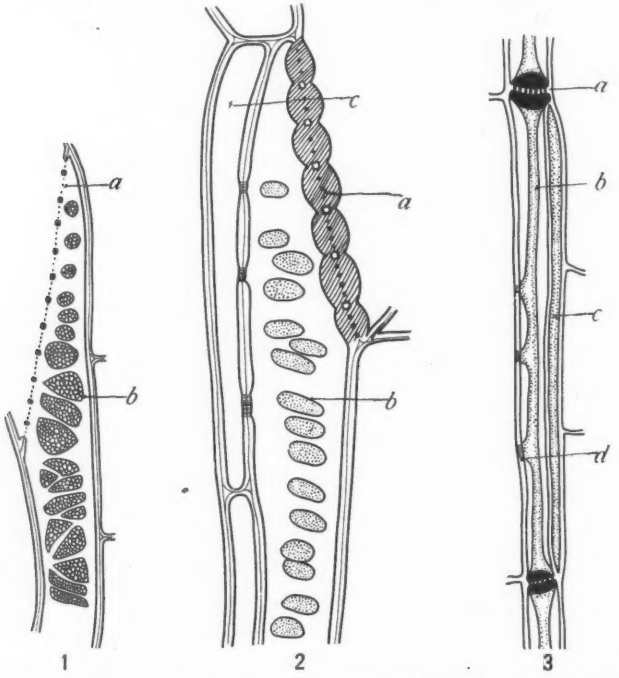
Fig. 4 is a transverse section of the stem of *Ranunculus fasciculatis;* the central, lighter portion of the three bundles shown here is phloem. Fig. 5 is a similar view of *Chenopodium album*, and fig. 6, of *Amaranthus paniculatus*. The darker areas just above the groups of large vessels are phloem. This peculiar, scattered arrangement of bundles in a woody cylinder would suggest a possible point of origin for the monocotyledons.

Companion cells are rare if not wanting in many of the lower dicotyledons. It is probable that parenchyma cells play the part of companion cells here.

The end walls of the ray cells in the phloem of some woody dicotyledons show sieve-platelike pitting, but they did not show any callus formation. This formation is easily observed in tangential sections of *Phellodendron*, *Rhus*, *Ilex*, *Acer*, *Gymnocladus*, *Acanthopanax*, and many other species. There are often thick-walled, unlignified, phloem-parenchyma cells in both woody and herbaceous dicotyledons that show lateral sieve-platelike pittings, but no terminal sieve-plates or callus were seen.

In the herbaceous dicotyledons studied, often the most striking

feature was the relatively small amount of phloem present. In *Paeonia* and *Thalictrum*, for example, there may be only 6–12 sieve-tubes in a bundle having perhaps 30–50 times that number of xylem elements; but often in woody plants only a few rows of sieve-tubes, as seen in radial section, are really functional.



FIGS. 1–3.—Fig. 1, one-third of a sieve-tube of *Juglans nigra: a*, end sieve-plate in cross-section; *b*, lateral sieve-plate in face view; fig. 2, one-half of a sieve-tube of *Vitis labrusca: a*, end sieve-plate in cross-section: *b*, lateral sieve-plate in face view; *c*, companion cell; fig. 3, full length view of a sieve-tube of *Lactuca scariola: a*, end sieve-plate in cross-section, with callus; *b*, slime contents; *c*, companion cell; *d*, lattice or "sieve-field."

No lignification of the phloem was observed in *Helianthus*. Perhaps the material used was collected too early or grew under different conditions from that described by BOODLE.[5]

[5] BOODLE, L. A., Lignification of phloem. Ann. Botany **16**: 180. 1906; also *ibid.* **20**: 319–321. 1910.

Species of over 140 genera, belonging to more than 60 families, have been studied. The sieve-tubes found in these different species, for the sake of convenience, may be grouped under three types, though perhaps most of them will come naturally between the first and second or second and third types.

The first type is like that found in *Pinus*. Here the lateral sieve-plates are the same as the terminal ones, and the end walls are very oblique, extending from one-fourth to one-half the length of the sieve-tube. Text fig. 1 shows one-third of a sieve-tube of *Juglans nigra* as seen in tangential view. The lateral sieve-plates are seen in face view on the tangential wall, while the terminal sieve-plates are seen in transverse section. The lateral sieve-plates on the tangential walls of the sieve-tubes in *Juglans* are usually more irregular and thinner than those on the terminal or radial walls.

The second type is like the first except that the lateral sieve-plates are less well developed, and the end walls are less oblique, and have 2–10 sieve-plates each. This type may be illustrated by *Vitis* (text fig. 2). The figure shows one-half of a sieve-tube in tangential section. The end wall here has 7 sieve-plates covered with callus. Poorly developed sieve-plates are shown in face view on the tangential wall. On the left is a companion cell related to the sieve-tube by fine pits.

The third type has end walls that are nearly at right angles to the side walls, and has only one sieve-plate to each end wall. The sieve-tubes of *Lactuca scariola* illustrate this type (text fig. 3). This sieve-tube, though shown in full length view, was drawn to the same scale as the other text figures. The three lattices on the left relate it to another sieve-tube.

The species studied may be grouped under these types as follows:

FIRST TYPE[6]

Alnus incana, A. rugosa, A. oregana, Betula alba, B. lenta, B. lutea, Banksia Menziesii, Carya alba, C. ovata, Castanea dentata, Castanopsis chrysophylla, Casuarina Fraseriana, C. equisetifolia, Corylus americana,

[6] The nomenclature of GRAY'S *Manual* (Ed. 7) is followed as far as applicable; the names of plants indigenous to Oregon are those used in HOWELL'S *Flora of Northwest America*.

C. rostrata, Carpinus caroliniana, Drimys colorata, Fagus grandifolia, Juglans cinerea, J. nigra, Myrica asplenifolia, M. cerifera, Nothofagus Menziesii, Ostrya virginiana, Populus balsamifera, P. grandidentata, P. tremuloides, P. trichocarpa, Quercus alba, Q. Garryana, Q. Kelloggii, Q. nigra, Salix fragilis, S. nigra.

BETWEEN FIRST AND SECOND TYPES

Berberis aquifolium, Celtis occidentalis, Aesculus glabra, A. Hippocastanum, Acer Negundo, A. macrophyllum, A. rubrum, A. saccharum, Crataegus coccinea, C. Douglasii, Calycanthus floridus, Fraxinus americana, F. oregana, Hamamelis virginiana, Holodiscus ariaefolia, Hydrangea vestita, Liriodendron Tulipifera, Magnolia acuminata, M. Fraseri, Maclura pomifera, Morus rubra, Philadelphus Lewisii, P. grandiflora, Platanus occidentalis, Prunus serotina, Pyrus baccata, P. coronaria, Rosa gallica, Ribes sanguineum, Sassafras variifolium, Ulmus campestris, U. americana.

SECOND TYPE

Ailanthus glandulosa, Arbutus Menzesii, Catalpa bignonioides, Ceanothus sanguineus, Cephalanthus occidentalis, Cercis canadensis, Cladrastis lutea, Cornus Nuttallii, C. pubescens, Clethra alnifolia, Diospyros virginiana, Euonymus atropurpureus, Gymnocladus dioica, Gleditsia tricanthos, Ilex opaca, Kalmia latifolia, Lyonia ligustrina, Phellodendron amurense, P. japonicum, Robinia Pseudo-Acacia, Rhus glabra, R. Toxicodendron, Ricinus communis, Rhamnus cathartica, R. Purshiana, Sambucus glauca, Syringa vulgaris, Tilia americana, T. europaea, Vaccinium corymbosum, Vitis labrusca.

BETWEEN SECOND AND THIRD TYPES

Abutilon Theophrasti, Acanthopanax sessiliflorum, Actaea alba, Agrimonia gryposepala, Amaranthus paniculatus, Aquilegia formosa, A. vulgaris, Aralia spinosa, Asarum canadense, Asclepias syriaca, Chenopodium album, Clematis ligusticifolia, Brassica alba, Datura stramonium, Daucus Carota, Dipsacus sylvestris, Euphorbia Preslii, E. corollata, Filipendula rubra, Geranium sanguineum, Geum triflorum, Hibiscus Moscheutos, Hypericum perforatum, Humulus Lupulus, Impatiens noli-tangere, I. pallida, Knautia arvensis, Paeonia montana, Potentilia rivalis, Polanisia graveolens, Polygonum Douglasii, Raphanus sativus, Rumex occidentalis, Saponaria officinalis, Solanum nigrum, Thalictrum dasycarpum, Tropaeolum majus, Urtica gracilis, Verbena officinalis.

THIRD TYPE

Ambrosia artemisiifolia, Arctium minus, Aster novae-angliae, Bryophyllum calycinum, Cichorium Intybus, Cicuta maculata, Cucurbita maxima, Cyclamen latifolium, Eupatorium purpureum, Echinocystis lobata, Eryngium yuccifolium, Helianthus annuus, Heracleum lanatum, Hieracium venosum, Lactuca scariola, Liatris squarrosa, Linaria vulgaris, Lobelia cardinalis,

Lupinus polyphyllus, Melilotus alba, Monarda punctata, Oenothera biennis, Opuntia Rafinesquii, Phaseolus vulgaris, Phytolacca decandra, Physalis heterophylla, Primula sinensis, Sium cicutaefolium, Scrophularia marilandica, Silphium laciniatum, Sonchus oleraceus, S. arvensis, Stachys palustris, Tephrosia virginiana, Trifolium pratense, Verbascum Thapsus, Veronica scutellata, Xanthium spinosum.

The following monocotyledons were similarily studied, and all were found to have sieve-tubes of the third type.

Alisma Plantago, Arisaema triphyllum, Dracaena scandia, Iris versicolor, Monstera deliciosa, Polygonatum commutatum, Potamogeton heterophyllus, Sagittaria latifolia, Scirpus validus, Smilax rotundifolia, Typha latifolia, Zea Mays.

There are of course no sharp lines of division in grouping these species according to type; even in the same section there may be some variation. But in general there is no wide variation even with different genera of the same family, except where there are both woody and herbaceous genera; then the herbaceous ones showed the higher type, as for example in Rosaceae and Leguminosae. The sieve-tubes of the Leguminosae on the whole are of a higher type than those of the Rosaceae. The woody Rosaceae often have sieve-tubes about like the first type, with regular large lateral sieve-plates. While the woody Leguminosae may have occasionally well developed lateral sieve-plates, they are usually as small as in *Sambucus* or *Tilia*. The xylem of the Leguminosae has been likewise found to be a higher type, so perhaps these families do not belong so near each other as they are usually placed.

It will be noted that the woody dicotyledons studied are placed in the first and second types, while the herbaceous ones are in the intermediate type between the second and third, or in the third type. Three or four sieve-plates were the most seen on the end wall of any strictly herbaceous plant, as for example *Euphorbia* and *Thalictrum*. Even in these genera end walls with only one sieve-plate were often observed. In the Compositae studied, only one sieve-plate to each end wall of the sieve-tube could be found. When stained with Russow's callus reagent, the pores of the "sieve-fields" or lattices showed up as orange dots, but they never were large nor fused into callus pads.

Occasional lateral callus pads were observed in most of the

other herbaceous plants studied. In *Cucurbita maxima*, for example, as many as 9 lateral callus pads have been seen in a continuous row in a single sieve-tube.

The evolution of the sieve-tube parallels that of the tracheid or vessel. For example, in *Ephedra* the vessels have oblique end walls with several round or oval pits. This is supposed to be the primitive type of vessel. In *Liriodendron* the end wall of the vessel is still rather oblique, but the pits are of the scalariform type and close together. In the highest type, the pitted vessel, the little margin that is left of the end wall is usually at right angles to the side walls, as in *Fraxinus*.

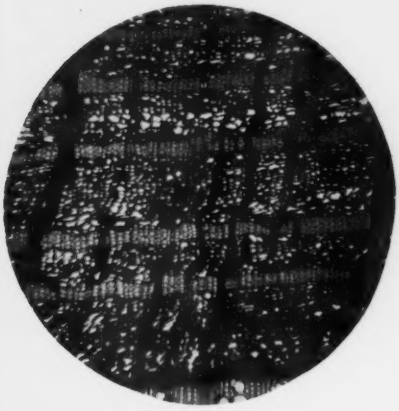
Conclusion

In studying the phloem of the dicotyledons, it has been found that there is a gradual transition from the gymnospermous type of sieve-tube to the so-called dicotyledonous type as seen in the Compositae. At the first stage in advance the lateral plates are smaller and have smaller meshes than the terminal plates; then as the terminal wall becomes more and more at right angles to the lateral walls, the number of terminal plates decreases until there is only one terminal plate with relatively large meshes, and the lateral plates become "sieve-fields" or lattices.

Paleobotany, ontogeny, and studies of xylem have induced many botanists to believe that herbaceous plants are more advanced in their evolutionary development than woody plants. This study of the sieve-tube adds another argument in favor of this view.

The first two years of this work were done in the Phanerogamic Laboratory of Harvard University under the direction of Professor E. C. JEFFREY, and the last year of work has been under the direction of Professors J. M. COULTER and W. J. G. LAND at the University of Chicago. The writer wishes to express his thanks to these instructors for their helpful advice.

TRANSYLVANIA UNIVERSITY
LEXINGTON, KY.



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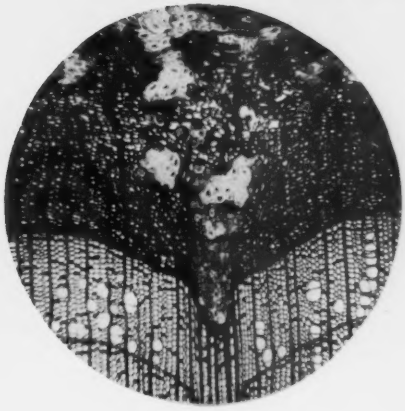

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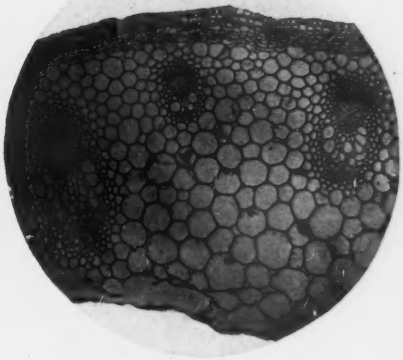

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HEMENWAY on SIEVE-TUBES

EXPLANATION OF PLATE XI

FIG. 1.—Transverse section of phloem of *Acer macrophyllum*, showing horizontal bands of hard bast and general view of sieve-tubes and parenchyma cells.

FIG. 2.—A similar view of *Alnus incana*, showing that the hard bast occurs chiefly opposite the aggregate rays.

FIG. 3.—A similar view of *Quercus Garryana*, showing distribution of hard and soft bast.

FIG. 4.—Transverse section of stem of *Ranunculus fascicularis*, showing scattered bundles and relatively small amount of phloem.

FIGS. 5 and 6.—*Chenopodium album* (fig. 5) and *Amaranthus paniculatus* (fig. 6), showing peculiar scattered bundles that might suggest relationship to the monocotyledons.

PARAFFIN BLOCKS FOR GROWING SEEDLINGS IN LIQUID CULTURE SOLUTIONS[1]

CONRAD HOFFMANN

(WITH THREE FIGURES)

In growing seedlings of any kind in nutrient solutions a suitable means of supporting the individual plants is essential. The method commonly employed consists in the use of ordinary corks perforated so as to hold a varying number of seedlings. Invariably the corks are of such a size as to fit snugly in the neck of the vessel containing the nutrient culture solution. This apparatus, while satisfactory to a certain extent, offers several objections. The corks usually discolor the nutrient solution, the extent of discoloration depending upon the grade of cork employed, as well as upon the composition of the nutrient solution. This discoloration is due to soluble compounds, presumably organic in nature, which can be inferred to have some influence—beneficial or detrimental—upon the growing seedlings. The corks soon warp and crack and become unfit for further use. Further than this, they furnish a substratum for molds, which frequently give trouble by infecting the seedlings to be grown.

These were some of the objections and difficulties encountered in the course of certain experimental work with growing seedlings. It was necessary in this work to grow a large number of seedlings in different culture solutions, which necessitated the employment of a large number of supports. The support which was finally adopted after considerable experimentation proved so satisfactory as to warrant its description and publication at this time.

In place of the ordinary cork a paraffin block molded in the desired shape and size and perforated to suit the needs of the experiment has been used. It has been found advisable to employ a paraffin of comparatively high melting point, so as to prevent any melting or softening of the blocks under the direct rays of the sun to which they will be exposed in the course of their use.

[1] Published with permission of Director of Wisconsin Experiment Station.

To obtain blocks of the desired thickness and size, the following procedure has proved most effective. The paraffin is placed with sufficient distilled water in a suitable vessel and boiled vigorously. The paraffin can then be removed from the surface of the water

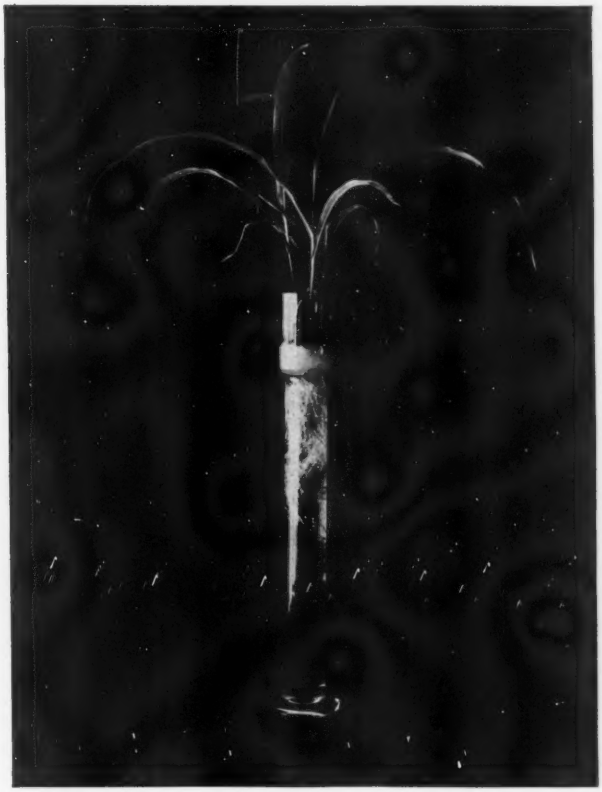

FIG. 1.—Showing use of paraffin block and hydrometer cylinder for growing seedlings in nutrient solutions.

and poured into a large cylindrical mold. This mold is best made out of some heavy paper and can be made of any desired diameter. After solidification of the paraffin within this mold, the various-sized cylinders can be cut off in much the same manner that bread

is cut. These cylindrical blocks can be made of any thickness, and by varying the size of the mold can be made of any diameter. To render the cutting of the paraffin more satisfactory, the mold can be placed at a temperature of 30–35° C., which will be sufficient to keep the paraffin in a pliable condition. Another method for securing these blocks which has given good satisfaction is to pour the hot water and paraffin into shallow pans, forming a layer of paraffin above the water of any desired depth, and then allowing it

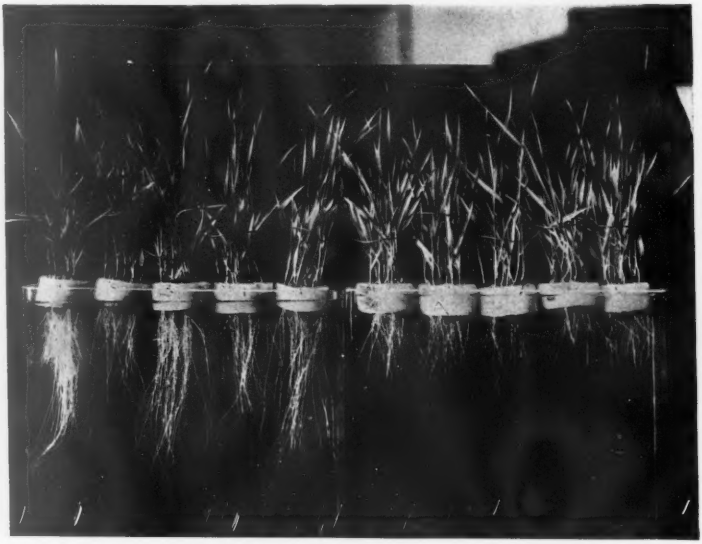

FIG. 2.—Seedlings in paraffin blocks suspended in water to show root development

to solidify. From the circular layer thus secured, the desired blocks can be cut with various-sized cake cutters.

The blocks of paraffin thus secured are then perforated in one of two ways. In the one the ordinary cork-borer is employed, using two of different diameters, making a perforation with the smaller through the entire block, and then with the larger borer through the upper portion of the block. In this way a perforation is secured with a small shelf upon which the germinating seedling can be placed. Equally satisfactory has proved the method of

using a piece of ordinary glass tubing which has been drawn out in a conical form. By pushing this through the paraffin a perforation is secured which is larger at the top and smaller at the bottom of the block, and which will prevent the seed from falling through into the liquid in which the paraffin blocks are to be suspended. In this manner one can make a support of any size and with as many perforations as desired. These blocks when placed in the liquid culture medium serve automatically to keep the roots immersed

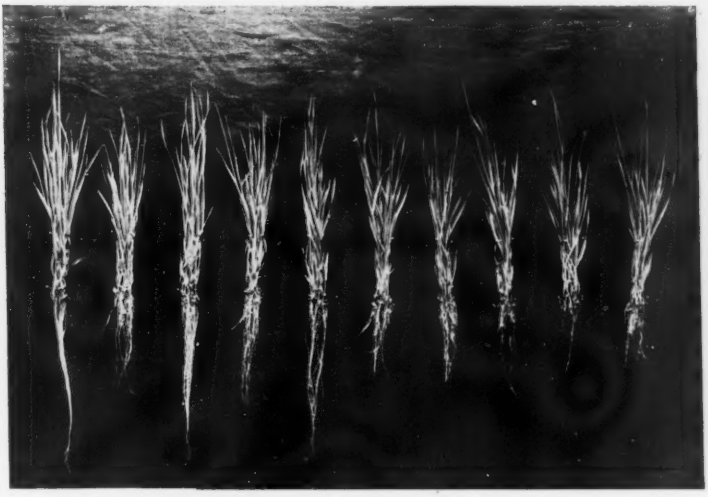

FIG. 3.—Same seedlings as in fig. 2, but removed from water; far less differentiation in root development is evident.

in the liquid, since they are free to rise and fall with variations in the level of the nutrient solution. This is impossible with a cork which fits snugly in the neck of the vessel, unless one continually restores the water lost by transpiration and evaporation.

The size of the block, as well as the perforations, will depend entirely upon the seedlings to be grown, making them large for peas and corn, and small for wheat and clover. The blocks thus prepared can be floated upon the culture medium in which the seedlings are to be grown, and, as already stated, will rise and fall

with changes in the elevation of the nutrient solution. Sufficient bulk must be given to the blocks to provide for the increased weight resulting from the growth of the plant.

The most suitable receptacle for floating these block cultures has been found in the form of an ordinary hydrometer cylinder which has the enlargement at the upper portion of the cylinder. This is well shown in the accompanying illustration (fig. 1).

For photographic purposes of seedlings thus grown these floats with their burden are placed in large, flat, glass vessels similar to the rectangular museum jars which are now being employed. In this way the root systems are well distributed and give a photograph revealing any differences which may exist in the root development. A comparison of the two photographs submitted (figs. 2 and 3), the one taken as above described, the other after removal from the water demonstrates this feature very strikingly, and proves the advantages of photographing as described. This method of photographing is considered worthy of employment where work of a similar nature is performed and presented.

AGRICULTURAL BACTERIOLOGICAL LABORATORIES
UNIVERSITY OF WISCONSIN, MADISON, WIS.

BRIEFER ARTICLES

A SIMPLE REVOLVING TABLE FOR STANDARDIZING POROUS CUP ATMOMETERS

(WITH ONE FIGURE)

In connection with field work carried on during the past season the writer has had occasion to standardize nearly 70 porous cup atmometers of the type described by LIVINGSTON.[1] The necessity of exposing the various cups in a series to uniform atmospheric conditions during the standardizing process is readily comprehended, but the difficulty in securing such conditions can be fully appreciated only by those who have tried it. LIVINGSTON has recently described a rotating table for standardizing these instruments,[2] and so far as fulfilling the requirements is concerned this can scarcely be improved upon. The only objection to it is the amount of time and expense involved in its construction, an objection which may have considerable weight if what is needed is a makeshift contrivance for temporary or perhaps occasional use rather than a durable piece of permanent equipment. The writer has devised for his purpose a very simple type of revolving table which can be constructed from readily obtainable materials with very little labor and expense and which has proven very serviceable.

This apparatus is shown in the accompanying photograph (fig. 1). It consists, in brief, of the front wheel of a bicycle suspended horizontally within a wooden framework; on the upper side of the wheel is laid a piece of thick cardboard, or pulpboard, to support the bottles; from the lower side of the wheel wooden vanes are hung perpendicularly; the wheel is then caused to rotate by means of an air current from an electric fan. For constructing the framework three-quarter inch pine board is sufficiently heavy, and rigidity is insured by the use of braces at the angles; the dimensions are largely a matter of convenience and will naturally depend somewhat on the diameter of the wheel used, height of atmometers, size of vanes, etc.; the framework shown in the figure measures 36×30×24 inches (inside height, inside width, and depth, respectively). For supporting the wheel two upright pieces are

[1] Carnegie Institution of Washington, Publication No. 50. 1906.

[2] Plant World **15**: 157–162. 1912.

used; one of these projects vertically upward from near the center of the base of the framework (see fig. 1) to a level somewhat less than halfway to the top; the other projects downward from the top of the framework, in line with the first, to a level somewhat less than halfway to the bottom; the distance between the two contiguous ends of these uprights should be slightly greater than the length of the wheel hub; both uprights should be firmly braced. The wheel is held in position between the two uprights by means of two iron "corner-braces" (which can be secured at any hardware store), in each of which one of the four screw holes has been bored large enough to fit the axle of the wheel. In adjusting the

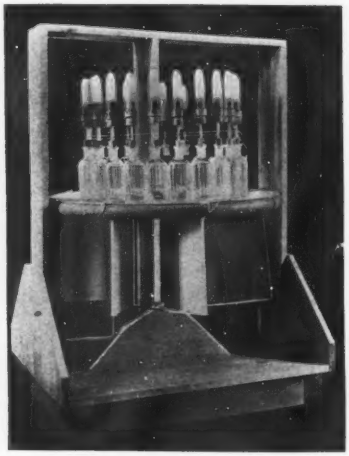

FIG. 1

wheel to position a corner-brace is first screwed vertically to the upper end of the lower upright; the wheel is set in this and then firmly fixed in place by means of the second corner-brace which is screwed to the lower end of the upper upright; any slight divergence of the wheel from the horizontal plane can be corrected later by tilting the entire framework. For vanes 8 pieces of light wood about 8×10 inches are used; these are attached to the spokes by means of screw-hooks, being hung at a slight angle to the radii of the wheel; they are tied to the rim at their upper edges and are further held in position by means of wooden strips tacked to their lower edges. This table will accommodate 20 or more atmometers. As a precaution against the possibly disastrous

effect of centrifugal force it is well to fasten a cord around the bottles after the manner shown in the figure. The velocity at which the table rotates can be controlled by regulating the position and angle of the fan with respect to the vanes. If the bearings of the wheel are properly adjusted and the table with its load carefully balanced, a speed of less than four revolutions per minute can be maintained. The direct air current from the fan should not strike the cups.

Such a revolving table as the one here described was run in the writer's laboratory almost continuously for nearly three weeks at a speed ranging from 4 to 20 revolutions per minute and gave no trouble whatever. In order to determine the accuracy of the data obtained, a test series of 20 cups was operated under various conditions for more than a week, readings being taken daily. It was found that with the table revolving at a rate of 8 revolutions or less per minute the coefficients derived from the readings of consecutive days varied very little; for several days none of the cups showed a variation amounting to as much as one per cent, while the difference in evaporation between two standard cups amounted to less than 0.2 per cent. With increased speed, however, the coefficients are apt to fluctuate, due to various causes.—G. E. NICHOLS, *Yale University*.

POISONING BY GINKGO

Several botanists after dissecting the fruits of *Ginkgo* have developed what appeared to be ivy poisoning. As the juice of the *Ginkgo* produced an immediate irritation of the skin, it was suspected that the rash which developed the following day was due to this. Later tests proved this to be the case. The poison is in the outer fleshy layer. It does not affect all people, since the gardeners at Smith College and at Mount Holyoke College have never been poisoned by handling the *Ginkgo* fruits, but a gardener in Elyria, Ohio, who cares for a fruiting tree in the yard of Mr. WILLIAM G. SHARP, writes that he is poisoned every fall by handling the fruits. The irritation produced is greater than that of poison ivy, and the infection spreads more persistently and is communicated from one person to another. Pustules rarely form, however, as in ivy poisoning, but there is a heavy red rash, attended by the formation of welts in severe cases.—ANNA M. STARR, *Mount Holyoke College, South Hadley, Mass.*

CURRENT LITERATURE

BOOK REVIEWS

Parasitic seed plants

In order to place at the command of students and teachers the best known methods of growing parasitic seed plants and to encourage the introduction of these hitherto neglected organisms into botanic gardens, HEINRICHER[1] has compiled from his wide experience a manual of explicit directions for the culture of all the better known species. Most of the European and many of the foreign representatives of the Scrophulariaceae, Orobanchaceae, Convolvulaceae, Lauraceae, Santalaceae, Loranthaceae, and Rafflesiaceae are included in his rather extensive list, and in nearly every instance his suggestions are based upon personal experience extending over several years. His previous investigations of the peculiarities in the germination of the seeds of parasites (reviewed in this journal[2]) have been extended, and much valuable data collected on the time required for bringing the parasites to maturity, as well as to the particular host upon which each develops best. While many of these plants may be grown readily in the open ground, pot culture is recommended for others on account of the greater ease with which they may be protected from insects and other enemies. It is found that many of the green hemiparasites are not very exacting in their choice of a host, but in promoting vigorous and rapid development care is often necessary in selecting a host that will not by too vigorous growth exclude the sunlight from the foliage of the parasite. This would indicate that the dependence is here incomplete and that carbohydrates are synthesized by the leaves of the parasite. HEINRICHER, however, does not rely upon this evidence alone to demonstrate that many of the green parasitic seed plants, particularly those of the Rhinanthaceae, obtain only water and nutritive salts from their hosts, but produces what seems to be a most complete line of evidence in support of his contention[3] that photosynthesis continues long after the evolution of the parasitic habit has begun. He presents evidence that the leaves of these plants are highly differentiated morphologically, possess abundant stomata,

[1] HEINRICHER, E., Die Aufzucht und Kulture der parasitischen Samenpflanzen. 8vo. pp. 53. Jena: Gustav Fischer. 1910.

[2] BOT. GAZ. **49**:391. 1910.

[3] HEINRICHER, E., Die grünen Halbschmarotzer, VI. Zur Frage nach der assimilatorischen Leistungsfähigkeit der grünen parasitischen Rhineanthaceen. Jahrb. Wiss. Bot. **47**:539–587. 1910.

show a periodicity in their starch content which coincides with the recurrence of daylight and darkness, that locally darkened areas of the leaf blade soon show a deficiency in starch content, and that when the stomata are closed with cocoa butter starch formation does not occur. Further it appears that shoots free from starch soon showed the presence of that substance if placed in sunlight in an atmosphere containing CO_2, but controls, also in sunlight but in an atmosphere without CO_2, showed no starch. Support is also given to the contention that many of these plants receive no carbohydrates from their hosts by the fact that they will thrive as root parasites upon annuals which have no starch or sugar stored in their subterranean organs.—GEO. D. FULLER.

Phosphorescence in plants

MOLISCH[4] has issued a second and enlarged edition of his work on phosphorescing plants. The book is very simply and interestingly written, and brings up to date his own extensive work in this field as well as the work of all other investigators. The first chapter answers negatively the question "are there phosphorescing algae?", and shows that such appearances are due to light reflection or to animals living on the algae. The second chapter gives the evidence for the existence of phosphorescence in marine Peridineae and for its absence in fresh water forms. The third chapter deals at length with the phenomenon in fungi, both Hyphomycetes and bacteria, and the fourth shows the relation of salts and temperature to the light production in bacteria. The fifth treats of the nutrition, phosphorescing, and growth of the light-producing fungi, and the sixth with the manner in which light is produced. Phosphorescence is an oxidation process demanding a minimal though very small partial pressure of oxygen. There is no convincing evidence for any direct relation between respiration and phosphorescence, much less for the latter being produced by the former. The living cell produces a substance, photogen, which phosphoresces in the presence of water and free oxygen. In the higher fungi and bacteria, in contrast to many animals, the phosphorescing has never been obtained extracellularly. In chapter seven the author gives the spectra and other characters of the light produced by various fungi.

The bacterial light is of sufficient intensity and of proper quality to render photographic work possible by it as the sole source of light. It will cause heliotropic response in various seedlings and fungi, and lead to chlorophyll production, detectable by the spectroscope though not sufficient for visible greening. The light is not capable of penetrating opaque objects, as some workers have probably wrongly claimed for light produced by various animals.

In contrast to the situation with many animals, MOLISCH cannot discover any biological significance of light production in plants. The last chapter

[4] MOLISCH, HANS, Leuchtende Pflanzen, eine physiologische Studie. viii+193. *pls. 2. figs. 18.* Jena: Gustav Fischer. 1912.

deals with the alleged phosphorescence in flowering plants, and concludes that the cases cited are either counterfeit or due to electrical phenomena (St. Elmo's fire).—WILLIAM CROCKER.

MINOR NOTICES

The nuclei of Protista.—The name "Protista," applied by HAECKER to the lowest animals and plants, has failed to receive general acceptance, even among zoologists, and the forms are found under both the protozoa and unicellular plants. In any consideration of the phylogeny of the nucleus these forms must be of great interest, because the nuclei of the metazoa and of the higher algae and fungi are too highly differentiated to throw much light upon such a subject as the origin of the nucleus. A paper by HARTMAN[5] deals almost entirely with the nucleus of protozoa and its significance as the forerunner of the nucleus of the metazoa. Botanists working with the nucleus in the lower algae and fungi, and especially with flagellates, cannot afford to overlook this paper.—CHARLES J. CHAMBERLAIN.

Symbolae Antillanae.[6]—In continuation of this important work Professor URBAN in cooperation with several eminent specialists has issued the second and third fascicles of the seventh volume. There are included descriptions of approximately 300 new species, several varieties, and a few new combinations. The following new genera are proposed: *Sarcopilea* of the Urticaceae, *Plethadenia* of the Rutaceae, *Hypocoton* of the Euphorbiaceae, *Ottoschulzia* of the Icacinaceae, *Maga* of the Malvaceae, *Poicillopsis* of the Asclepiadaceae, *Tuercklæimocharis* of the Scrophulariaceae, and *Shaferocharis* of the Rubiaceae.—J. M. GREENMAN.

NOTES FOR STUDENTS

Root-tubercles of non-leguminous plants.—In an extremely long and somewhat obscure article, which is not made any clearer by the vague illustrations accompanying it, PEKLO[7] gives an account of his studies of the organisms in the root-tubercles of *Alnus* and *Myrica*. With respect to the morphology of the organisms the author adds nothing to what is known from earlier accounts, especially the excellent account of SHIBATA with which he agrees in all essential details. PEKLO finds in the cells of the root-swellings of *Alnus* and *Myrica* masses of filaments with more or less radial arrangement and termi-

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[5] HARTMAN, MAX, Die Konstitution der Protistenkerne und ihre Bedeutung für die Zellenlehre. 8vo. pp. v+54. *figs. 13.* Jena: Gustav Fischer. 1911.

[6] URBAN, I., Symbolae Antillanae seu fundamenta florae Indiae Occidentalis. Vol. VII, fasc. 2, pp. 161–304, 15 June; fasc. 3, pp. 305–432, 1 October. Leipzig: Fratres Borntraeger. 1912.

[7] PEKLO, J., Die pflanzlichen Aktimonykosen. Centralbl. Bakt. II. **27**:451–579. 1910.

nating in the peculiar vesicles described by BRUNCHORST. Like BRUNCHORST, he regards these vesicles as sporangia and describes the fragmentation of their contents into angular "spores." In the filaments themselves, which finally break up into segments, he finds deeply staining bodies described by SHIBATA, and which resemble the spores of bacteria. These are regarded as endospores, although in his subsequent cultural work he appears to have made no attempt to settle the question of the sporelike nature either of these bodies or of the fragments of the vesicles, by showing that they are capable of germination. In view of SHIBATA's observation that these bodies as well as the filaments are completely absorbed by the host, it seems that an experimental attempt to determine their true nature would have been worth while, especially since the author seems to have found no difficulty in growing his organisms. The characteristics of the organisms in cultures from both *Alnus* and *Myrica* were similar to those observed in the host cells. The indecisive results of the infection experiments, however, leave some doubt as to whether his cultures contained the causal organisms of the root-galls. From the resemblance of the root-gall fungus of *Alnus* and *Myrica* to the animal parasite *Actinomyces*, PEKLO, following a suggestion made by SHIBATA in regard to the fungus of *Myrica*, transfers these organisms to the genus *Actinomyces*, and rebrands the galls, *Actinomycoses*. All these organisms he believes are highly organized bacteria.

BOTTOMLY[8] studying the root nodules of *Myrica Gale* finds that the bulk of the cortical tissue back of the meristem of the growing apex of the young nodules is infected with bacteria. These are massed together in "infection threads" extending from cell to cell. The bacteria were obtained in pure cultures where they showed the characteristics of *Pseudomonas radicicola*. Cultures grown for seven days at 25° C. showed a fixation of 2.05 mg. nitrogen per 100 cc. It was found that *Myrica* plants growing in sterilized soil deficient in nitrogen did not flourish unless they possessed root nodules. When plants free from root nodules and growing poorly were watered with a culture of the bacteria, nodules developed and the plants began to thrive. Fungus filaments are found in the older parts of the galls, sometimes close to the bacteria-infected cells, but although not denying the possible mycorhizal nature of these filaments which are the organisms described by previous investigators, he believes that they have nothing to do with the origin of the nodules or with nitrogen fixation.

Miss SPRATT[9] confirms former observations of BOTTOMLY, according to which the root-gall organisms of *Alnus* and *Elaeagnus* is a bacterium identical with *Pseudomonas radicicola*. The organism occupies the young cortical tissues

[8] BOTTOMLY, W. B., The root nodules of *Myrica Gale*. Ann. Botany **26**: 111–117. 1912.

[9] SPRATT, ETHEL ROSE, The morphology of the root tubercles of *Alnus* and *Elaeagnus*, and the polymorphism of the organism causing their formation. Ann. Botany **26**: 119–128. 1912.

in a manner similar to that of the organism of *Myrica* described above. Miss SPRATT also finds that under certain conditions, both in the root and in cultures, the organism gives rise to relatively large spherical bodies or coccus forms. This polymorphism seems to be the result of lack of nutrition. When nutriment is supplied they divide and become transformed into typical bacilli. It was also shown that the organisms from both plants were capable of fixing free nitrogen, thus confirming HILTNER'S observations.—H. HASSELBRING.

Morphology of orchids.—VERMOESEN[10] has made a careful study of the development of the ovule in several orchids. He finds arising at the lines of fusion of the three carpels three longitudinal "primary placental protuberances," each of which is caused by the enlargement of a band of subepidermal tissue, usually appearing in cross-section as three cells (possibly from a single one). The lateral members of this band of cells continue to divide actively, while in the median line growth is retarded, resulting in a bifurcation of the placental protuberance. Growth is further checked at various transverse levels, so that the ovary wall soon shows three double rows of small prominences, each with its isolated group of active subepidermal cells. These prominences now branch repeatedly to form the numerous ovulary filaments, each of which finally produces an ovule at its summit. All the steps of this process are initiated by the activity of the subepidermal cells, which retain the characters of archesporial tissue.

The author's main conclusion is that the primary archesporial cells are those which give rise to the original placental protuberance on the wall of the ovary, since this group of cells by repeated dichotomy gives rise to all the tissue within the branched placenta, funiculus, and nucellus. The sterilization idea is extended to include all these organs. It is further held that each carpel originally produced on its ventral surface two marginal archesporial bands which have become fused with those of the neighboring carpels.

The development of an eight-nucleate embryo sac from one megaspore of an "incomplete tetrad" and fertilization occur in the usual manner.—LESTER W. SHARP.

Dioecism in Epigaea.—The flowers of *Epigaea repens* were divided by GRAY into two main groups: one with well developed stigmas and abortive stamens, and the other with small, poorly formed stigmas and well developed stamens. Both groups possess equally good ovaries and ovules, and both show stamens and pistils of various lengths. STEVENS[11] has undertaken to determine two points: (1) whether there is any real evidence of a heterostylic condition, and (2) whether the species is actually dioecious. He finds that

[10] VERMOESEN, CAMILLE, Contribution à l'étude de l'ovule, du sac embryonnaire, et de la fécondation dans les angiospermes. La Cellule **27**:115–162. *pls. 2.* 1911.

[11] STEVENS, NEIL E., Dioecism in the trailing arbutus, with notes on the morphology of the seed. Bull. Torr. Bot. Club. **38**:531–543. *figs. 4.* 1911.

pollen from stamens of all lengths develops readily on the stigmas of all lengths of pistil, provided the stigmas are of the well formed sort. From this and anatomical evidence he concludes that *Epigaea* is not truly heterostylous. With regard to dioecism, it was found that pollen develops readily upon the well formed stigmas, but not at all upon the poorly formed sort, although ovules with normal embryo sacs are present in the ovaries. Thus the flowers with small stigmas are apparently perfect but are functionally male, and the species is functionally dioecious. The author has also recorded some interesting facts concerning the development of the seed. The embryo sac is of the usual eight-nucleate type, and is surrounded by a layer of "tapetum" except at the much prolonged micropylar end. There is no period of free nuclear division in the development of the endosperm, transverse walls at once separating the sac into four chambers, in all of which the further cells divisions occur rapidly. When the endosperm is well developed it produces at each end a knoblike haustorial outgrowth which extends into the tissue of the integument. —LESTER W. SHARP.

Crown-gall.—In their account of the crown-gall of plants, SMITH, BROWN, and TOWNSEND[12] described the occurrence of secondary galls originating at some distance from primary galls which had been produced by direct infection, and suggested that the secondary galls arose in some way from the primary galls, although the mode of origin was not clear at that time. This problem has now been solved by a histological study of the crown-gall by SMITH, BROWN, and MCCULLOCH.[13] They find that the secondary galls arise from strands of tissue which originate from the primary galls and make their way along the stem or leaf, usually in the region of the primary wood. The tumor strand apparently does not absorb the cells in its path, but makes its way by crushing and flattening them. Secondary galls arise at various points along the tumor strand. A cross-section of a secondary gall developing in the leaf from a strand arising from a primary gall in the stem shows a stem structure with the woody elements greatly developed and regularly arranged like the secondary wood of a stem. If, however, a primary gall develops in the leaf as a result of direct inoculation, its structure is irregular. The tissue consists of an enormous development of parenchyma intermixed with irregular masses of tracheids. There is no distinct differentiation of parts as in the secondary galls arising from stem galls. The similarity which has been formerly pointed out between these plant galls and animal tumors leads the writers to consider the crown-gall apart from all other plant diseases, and to place it in the category of true tumors.—H. HASSELBRING.

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[12] Rev. BOT. GAZ. **52**:75. 1911.

[13] SMITH, ERWIN F., BROWN, NELLIE E., and MCCULLOCH, LUCIA, The structure and development of crown gall; a plant cancer. Bur. Pl. Ind. Bull. 255. pp. 60. *figs.* 2. *pls.* 109. 1912.

Comparative anatomy of stomata.—From an examination of over 30 species of seed plants, taken from widely scattered genera, WARNCKE[14] finds upon many very divergent forms of stomata upon the different organs. So marked is the diversity that in some instances each organ seemed to possess its own particular type. On the whole, however, stomata on stems and petioles are much alike and are usually larger and with thicker walls than those of foliage leaves. The most divergent forms are those occurring upon rhizomes and in the epidermis of the inner side of sheaths. The very different external conditions will at least partially account for the greater amount of submergence below the level of the epidermis, for the thicker cell walls of the stomata of more exposed organs, and for the tendency toward loss of function and suppression upon the submerged and subterranean parts, but it is quite inadequate to explain the occurrence of two such entirely diverse types as those found upon the outer and inner surfaces of the sheath of *Zea Mays*. As might be expected, a close relationship is found to exist between the type of stomata and the general outline of the epidermal cells.

No phylogenetic sequence is revealed in the various forms examined; indeed, the investigator does not believe that PORSCH[15] is warranted in his conclusions regarding the phylogenetic importance of the types of stomata, since he compared as homologous the stomata of various organs now found to differ to a marked degree upon the same individual, and even, in a few instances, upon different parts of the same organ.—GEO. D. FULLER.

Embryo sac of Crassulaceae.—In 1908 WENT described the ovule and embryo sac of the Podostemaceae, in which he found among other peculiarities an empty cavity or "Pseudoembryosack" extending from the base of the short sac to the chalazal region. This has led Miss ROMBACH[16] to investigate the related Crassulaceae in the hope of throwing some light upon the significance of this peculiarity. Eight species were examined, which showed agreement in all essential features. A subepidermal cell of the very reduced nucellus cuts off one parietal cell and then divides to form four megaspores, the innermost of which gives rise to an embryo sac of the ordinary eight-nucleate type. During the early development of the endosperm and embryo the base of the sac with the antipodals grows downward through a central strand of loose, elongated cells until it reaches the chalaza.

The author believes that here are present side by side two processes: the outgrowth of the embryo sac, and cavity formation by the nucellus. In the Podostemaceae it is supposed that the embryo sac formerly filled all the

[14] WARNCKE, FREDERICK, Neue Beiträge zur Kenntnis der Spaltöffungen. Jahrb. Wiss. Bot. **50**: 21–66. 1911.

[15] PORSCH, O., Der Spaltöffungsapparat im Lichte der Phylogenie. Jena. 1905.

[16] ROMBACH, SARA, Die Entwicklung der Samenknospe bei den Crassulaceen. Rec. Trav. Bot. Neerlandais **8**: 182–200. *figs. 10.* 1911.

cavity down to the chalaza, as in the Rosaceae, but for some reason, possibly as a result of the peculiar mode of life shown by these plants, the outgrowth process no longer occurs, so that the empty "Pseudoembryosack" remains. The Crassulaceae are thus regarded as transitional forms between the Podostemaceae and the Rosaceae.—LESTER W. SHARP.

Antarctic lichens.—In 1909 DARBISHIRE[17] reported on the very extensive collection of lichens secured by the Norwegian polar expedition of 1898–1902 under NANSEN. In connection with this report it was shown that from the region including Arctic America, Greenland, Spitzbergen, and Iceland about 500 lichens have been recorded. A similar report has now been published by DARBISHIRE[18] for the antarctic region, based upon the collection brought back by the Swedish antarctic expedition of 1901–1903. There are now known 534 lichens from the general antarctics (subantarctic America, South Georgia, and the true antarctic region), 145 of which were secured by the expedition, 34 of them being new species. The true antarctic region contains 106 known lichens. It is an interesting fact that the relation of arctic to alpine lichens is much greater than that of subantarctic American species to those of New Zealand. It is further obvious that the similarity of subantarctic to arctic species is less striking than that of antarctic to arctic species, 43 per cent of the antarctic lichens being found in the true arctics and not in temperate regions.

The new species are distributed among 17 genera, *Lecidia* and *Buellia* having 5 each; *Pertusaria*, *Aspicilia*, and *Verrucaria* having 3 each; *Bacidia*, *Lecanora*, and *Parmeliella* having 2 each. The remaining genera, each represented by one new species, are *Biatora*, *Thelotrema*, *Placodium*, *Caloplaca*, *Pannoparmelia*, *Parmelia*, *Rinodina*, *Acarospora*, and *Chaetomium*.—J. M. C.

A new Williamsonia.—SEWARD[19] has studied petrified material of a *Williamsonia* from the Jurassic of Scotland, to which he gives the name *W. scotica*. It proves to be an exceedingly interesting and suggestive form. The most striking vegetative feature is the replacement of the usual scales (ramentum) of the Bennettitales by an abundance of very long hairs, such as occur on *Dioon edule* and other living cycads. The sections of the strobilus, the first obtained of a *Williamsonia*, are of special interest. The bisporangiate character is problematical, since no stamens were evident and NATHORST has shown that some species of *Williamsonia* were monosporangiate.

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[17] DARBISHIRE, OTTO V., Lichens collected during the second Norwegian polar expedition in 1898–1902. Publ. Soc. Arts and Sciences Kristiania. 1909.

[18] ———, The lichens of the Swedish antarctic expedition. Wiss. Ergebn. Schwed. Südpolar-Exped. 1901–1903. **4**: no. 11 (pp. 73). *pls. 3*. 1912.

[19] SEWARD, A. C., A petrified *Williamsonia* from Scotland. Phil. Trans. Roy. Soc. London B **203**: 101–126. *pls. 9–12*. 1912.

The interseminal scales and megasporophylls (stalks bearing terminal ovules), however, are of the *Bennettites* type, but much simpler in structure, although some of the simplicity may be due to immaturity.

It is refreshing to obtain the following statement from an English paleobotanist: "The morphology of the Bennettitean flower is still a problem to be solved, and the attractive hypothesis that would have us regard this dominant group of the Mesozoic era as a guide to the evolution of the class which now occupies the pre-eminent position in the vegetable kingdom, requires to be substantially strengthened before it can claim to have solved the mystery of the origin of the flowering plants."—J. M. C.

Cytology of seedless oranges.—OSAWA[20] has investigated the cytological situation in the two seedless oranges known as the "Washington navel" (*Citrus aurantium*) and the "Unshu" (*C. nobilis*), chiefly using *C. trifoliata* as a check species. After showing that spermatogenesis and oogenesis in *C. trifoliata* are as usual among angiosperms, he finds in both the seedless forms a strong tendency toward the disorganization of pollen mother cells and megaspores. In the "Unshu" there is every stage in the failure of pollen development from a failure in the differentiation of sporogenous tissue up to the reduction divisions. In the majority of cases, however, pollen grains are produced. In the "Washington navel," spermatogenesis in the majority of cases does not proceed beyond the mother cell stage. In both forms oogenesis usually proceeds to the formation of megaspores and then fails. As some normal embryo sacs are produced a few seeds were obtained; and the usual failure of seeds is due chiefly to the failure of embryo sacs rather than of pollen grains, especially in the case of the "Unshu." The chromosome numbers in this form are 8 and 16. In *C. trifoliata* it was discovered that fertilization occurs about four weeks after pollination, and the fertilized egg divides three or four weeks after fertilization.—J. M. C.

Pine-barrens of New Jersey.—A careful examination of geological evidence leads TAYLOR[21] to the conclusion that the pine-barrens of New Jersey coincide in distribution with the geological Beacon Hill formation, an area that has been uninterruptedly out of the water since the Upper Miocene, and has several times been more or less completely surrounded by water. This would make this plant formation by far the oldest in New Jersey. Its xerophytic character does not appear to harmonize well with such a theory, although the number of more or less endemic species would seem to demand a rather complete and extended period of isolation such as the submergence and glaciation

[20] OSAWA, I., Cytological and experimental studies in *Citrus*. Jour. Coll. Agric. Tokyo **4**:83–116. *fig. 1. pls. 8–12.* 1912.

[21] TAYLOR, NORMAN, On the origin and present distribution of the pine-barrens of New Jersey. Torreya **12**:229–242. 1912.

of adjacent territory would afford. The evidence offered of the large proportion of non-autophytic plants included in the pine-barren flora would tend to indicate a plant formation of considerable antiquity. The species from the far north in the pine-barrens are explained as having come down with the advancing ice sheets and having become isolated in bogs such as were probably to be found within the area in question during the glacial period. This evidence seems to add probability to the hypothesis, which seems to be the best yet offered in explanation of the peculiar flora of this interesting plant formation. —GEO. D. FULLER.

Origin of maize.—COLLINS[22] has been attacking the problem of the origin of maize by extensive cultures of the different types of maize, teosinte (*Euchlaena mexicana*), and teosinte-maize hybrids, through a period of seven years. The current view is that maize was derived from its nearest wild relative, teosinte. COLLINS concludes that it originated as a hybrid between teosinte and an unknown grass belonging to the Andropogoneae, a grass which resembled the earless varieties of pod corn (*Zea tunicata*). In enumerating the pronounced differences between teosinte and pod corn, he calls attention to the fact that in practically every case the characters of maize are intermediate. The origin of the maize "ear" has always been an interesting question. COLLINS regards it as the homologue of the central spike of the staminate inflorescence, but the central spike is quite as anomalous as the ear, and to account for it may call for the fasciation of simple branches of the inflorescence. In this sense, therefore, both opinions as to the nature of the maize ear (central spike or fasciation) may be right.—J. M. C.

Influence of adult on seedling.—HILL and DEFRAINE[23] have investigated the seedling structure of *Persoonia lanceolata* (Proteaceae) as a basis for the claim that the adult structure influences that of the seedling. The occurrence of polycotyledony among the Proteaceae is well known, and also the resemblance in the habit of some of them to the gymnosperms. The number of cotyledons in *P. lanceolata* ranges from three to five, and the authors are convinced that they have arisen by the splitting of two original structures. The details of the seedling structure further emphasize the close resemblance to the polycotyledonous gymnosperms, "a resemblance which is found not only in the general morphological configuration, but also in certain histological details and in the transition phenomena." The authors, of course, attach no phylogenetic significance to these similarities, but "the resemblance is considered as a striking instance of homoplasy in which the adult has influenced to a considerable extent the seedling."—J. M. C.

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[22] COLLINS, G. N., The origin of maize. Jour. Wash. Acad. Sci. **2**:520–530. 1912.

[23] HILL, T. G., and DEFRAINE, E., On the influence of the structure of the adult plant upon the seedling. New Phytol. **11**:319–332. *figs.* 9. 1912.

Vascular anatomy of Ophioglossaceae.—LANG[24] has been investigating the vascular anatomy of the three genera of Ophioglossaceae, and in advance of the publication of the full papers he has made a brief statement of his conclusions. It is becoming increasingly evident that the Ophioglossaceae are true ferns, and this return to the earlier views as to their relationships is emphasized by the present paper. The critical study of the anatomy of the stem and leaf trace led to the conclusion that there is "an essential similarity in plan of stelar construction between the Ophioglossaceae and the Coenopterideae" (Botryopterideae and Zygopterideae). There are also features in common with the Osmundaceae and Hymenophyllaceae. When one considers the gaps in our knowledge of the extinct forms, it is safer to suggest relationship in a general way than to be too specific, and this attitude LANG has taken. He is convinced, further, that in the Ophioglossaceae a protostele has developed intrastelar pith.—J. M. C.

Vegetative reproduction in Angiopteris.—It has been known for a long time that the leaf stalk of *Angiopteris* is differentiated into two regions, a basal portion bearing stipules, and a midrib bearing pinnae, the two regions being separated by an abscission layer. From material in the garden and from a study of large specimens in the forest, VAN LEEUWEN[25] records the following observations: the foliage leaf persists for about two or three years and then breaks off at the abscission layer, the leaf base remaining many years longer; after the leaf has fallen, four resting buds appear on the leaf base, and when it finally falls off, one or more of the buds begin to grow and many develop into new plants.

RACIBORSKI first noticed such buds in *Angiopteris;* the present account gives additional information from plants growing under natural conditions.—CHARLES J. CHAMBERLAIN.

Fossil prothallia.—MCLEAN[26] has added to our meager knowledge of paleozoic prothallia by describing two female prothallia from the Lower Coal Measures of England. One is that of the classic *Lagenostoma Lomaxii*, and it resembles closely the female gametophyte of modern gymnosperms, the radial arrangement of the tissues suggesting centripetal growth by "alveoli." This radial arrangement is lacking in such a gametophyte as that of *Lepidocarpon*. The other gametophyte is that of *Bothrodendron*, one of the lycopods. It is extremely well preserved, and strongly resembles the emergent and

[24] LANG, WILLIAM H., On the interpretation of the vascular anatomy of the Ophioglossaceae. Mem. and Proc. Manchester Lit. and Phil. Soc. **56**: no. 12 (pp. 14). *figs. 6.* 1912.

[25] VAN LEEUWEN, W. DOCTERS, Über die vegetative Vermehrung von *Angiopteris evecta* Hoffm. Ann. Jard. Bot. Buitenzorg **10**: 202–209. *pl. 18.* 1912.

[26] MCLEAN, R. C., Two fossil prothalli from the Lower Coal Measures. New Phytol. **11**: 305–318. *figs. 2. pls. 5, 6.* 1912.

flaring gametophyte of the water ferns, with the archegonia developed outside the spore. Since the female gametophyte of *Lepidocarpon* remains entirely within the megaspore, that of *Bothrodendron* represents a more primitive condition, in which the gametophyte is partly free from its spore.—J. M. C.

Cold air drainage.—In investigating the physical factors influencing the distribution of vegetation in the Santa Catalina Mountains, SHREVE[27] has found important differences in the temperature limits of stations at similar altitudes, but differently related to the ridges and valleys of the mountain slopes. These differences are shown to be due to valleys and cañons being frequently occupied by a stream of cooled air, and to amount to a difference in the mean minimum temperature equivalent to that usually experienced with an increase in altitude of 2350 feet. The influence of this cold air drainage seems to be most important in its effect upon the upward distribution of low-land species, and will do much to account for the higher range of these species upon the ridges and upper slopes of cañons.—GEO. D. FULLER.

Botryopterideae.—LIGNIER[28] has investigated *Stauropteris Oldhamia*, and its relations to the Botryopterideae, which he prefers to call Coenopterideae. Following the theory of the meriphyte, and including the sporangial structures, he reaches the conclusion that *Stauropteris* does not belong to the Coenopterideae, which represent an advanced group, but very near to the more primitive Primofilices. Incidentally he presents a "genealogical tree," which indicates that the Primofilices have given rise to three lines: (1) to the Coenopterideae (Botryopterideae) through *Stauropteris* as a start; (2) to the Marattiaceae through *Archaeopteris* and *Botrychium*, with a possible side branch leading to the Leptosporangiates; (3) to the Pteridosperms (Cycadofilicales).—J. M. C.

Standardizing atmometers.—The difficulties involved in subjecting a considerable number of atmometer cups to exactly similar conditions of temperature, humidity, and air movement for the period of time necessary for their standardization has caused LIVINGSTON[29] to devise a table rotating once per minute by means of a small electric motor belted to a reducing gear. The cups, mounted in suitable bottles, are placed near the outer margin of the table, and should a very high rate of evaporation be required an electric fan is made to furnish a current of air crossing the table. As the efficiency of the atmometer is largely dependent upon the accuracy of its standardization this device will prove helpful to ecological workers.—GEO. D. FULLER.

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[27] SHREVE, FORREST, Cold air drainage. Plant World **15**:110–115. 1912.

[28] LIGNIER, O., Le *Stauropteris Oldhamia* Binney et les Coenoptéridées à la lumière de la théorie du mériphyte. Bull. Soc. Bot. France **59**:1–33. *figs. 11.* 1912.

[29] LIVINGSTON, B. F., A rotating table for standardizing porous cup atmometers. Plant World **15**:157–162. 1912.

Water relations of plants.—In order to make clear the complex relationships which determine the moisture content of the growing plant and more especially to emphasize the artificial character of the distinction usually made between the organism and its environment, LIVINGSTON[30] has prepared an excellent schematic representation. It should prove a valuable aid to teachers of ecology and plant physiology in presenting this difficult topic. The general theory of physical causation is made to apply to all the organic phenomena involved.—GEO. D. FULLER.

Habitats of the red cedar.—HARPER,[31] in seeking for an explanation for the occurrence of *Juniperus virginiana* in very diverse habitats, finds one which he deems satisfactory in the sensitiveness of the tree to fire. Its prevalence upon limestone soils is noted and the conclusion is reached that "the cedar dreads fire more than it likes lime," and that it is found chiefly in areas which are rarely visited by forest fires. No experimental data are offered in support of this conclusion.—GEO. D. FULLER.

A new Jurassic fern.—THOMAS[32] has described from the Jurassic of England a new species of the *Stachypteris* of POMMEL (1847). In studying the affinities of the genus, he concludes that the structure of the sporangia and of the fertile spikes does not indicate any close affinities with the modern groups of ferns, but that it must belong to "a group of ferns intermediate in their characters between the Cyatheaceae and the Schizaeaceae."—J. M. C.

Embryogeny of Ranunculaceae.—In continuing his studies of the embryo of Ranunculaceae, SOUÈGES[33] has published a detailed account of the embryogeny of *Adonis*. The preceding parts have dealt with the Clematideae[34] and with *Myosurus*.[35] In *Myosurus* the sequence of events is very constant, while in *Adonis* it is very variable.—J. M. C.

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[30] LIVINGSTON, B. E., A schematic representation of the water relations of plants; a pedagogical suggestion. Plant World **15**: 214–218. 1912.

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[32] THOMAS, H. HAMSHAW, *Stachypteris Hallei*, a new Jurassic fern. Proc. Cambridge Phil. Soc. **16**: 610–614. *pl. 4.* 1912.

[33] SOUÈGES, R., Recherches sur l'embryogénie des Renonculacées. Anémonées (genre *Adonis*). Bull. Soc. Bot. France **59**: 474–482, 545–550. *figs. 224–269.* 1912.

[34] BOT GAZ. **51**: 480. 1911.

[35] BOT. GAZ. **54**: 264. 1912.

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